

THE EFFECTS OF INTRASPECIFIC GENETIC VARIATION ON THE DYNAMICS OF PREDATOR-PREY ECOLOGICAL COMMUNITIES

SAMUEL R. FLEISCHER, PABLO CHAVARRIA

ABSTRACT. Predator-prey interactions are ubiquitous in nature and have captured the attention of ecologists and mathematicians. Previous studies have focused on coexistence dynamics without taking into account phenotypic and genetic variation within a species. Recent ecological models have incorporated evolutionary variables in order to further understand predator/prey and competitive dynamics. General classifications of possible dynamics exist, but no previous model has provided enough flexibility to generate all dynamics. We formulate new models for coevolution in generalized ditrophic predator-prey systems by incorporating quantitative characters relevant to predation in both prey and predator. We study the impact of such trait variation by means of theoretical analysis and numerical simulations.

1. INTRODUCTION

Natural populations differ in size, morphology, physiology, and behavior. This genetic variation is a central and organizing theme of evolutionary biology [4]. Recent ecological models have incorporated evolutionary themes in various ways. Abrams and Matsuda introduced vulnerability as an evolutionary variable for a prey species. This model results in chaotic, cyclic, and stable dynamics under various conditions [7]. Saloniemi introduced quantitative traits in a coevolutionary model. Attack rate was defined as a linear function of these trait values [9]. This model also produces chaotic dynamics under certain conditions. More recently, Schreiber, Bürger, and Bolnick proposed an apparent competition model with Gaussian attack rate functions for an evolving generalist predator on two non-evolving prey populations [4]. In contrast with classical apparent competition theory, this model provided evidence that apparent competition can give rise to stable facilitation between under certain conditions. The variety of dynamics produced by incorporating evolutionary variables into purely ecological models is both ecologically and mathematically relevant.

All of the aforementioned models can be considered specific manifestations of Kindrik and Kondrashov's General Model of Coevolution [8], which describes a multitrophic ecological system of species, each of which may have a number of quantitative traits which affect each species' fitness. As derived by [6], if these evolutionary variables stay normally distributed, their evolution is proportional to the partial derivative of the fitness function with respect to that variable. In other words, evolution is always in the direction which increases the mean fitness of the population. Since community genetical changes occur over many generations, the

constant of proportionality is small, and so the evolutionary variables are considered to be “slow” variables. In contrast, ecological changes may happen within a single generation, and so the ecological variables (each species’ population densities) are considered to be “fast” variables. These differing timescales allow us to consider the General Model of Coevolution as two separate subsystems, the ecological and the evolutionary. In the context of the ecological subsystem, the evolutionary variables can be viewed as slowly changing parameters.

2. MODEL AND METHODS

Consider the ditrophic dynamics of u predator populations with densities $M_i = M_i(t)$, consuming v prey populations with densities $N_j = N_j(t)$, respectively ($i = 1, \dots, u$, and $j = 1, \dots, v$). Ecological parameters will be defined as functions of predator phenotypic values, m_i , and prey phenotypic values, n_j , of quantitative traits. We assume these traits can be measured in the same unit, or can be transformed into the same unit [9]. Assume predator traits are normally distributed with mean $\bar{m}_i = \bar{m}_i(t)$ and constant variances σ_i^2 , and prey traits are normally distributed with mean $\bar{n}_j = \bar{n}_j(t)$ and constant variances β_j^2 , i.e., their distributions are given by

$$(2.1) \quad \begin{aligned} p(m_i, \bar{m}_i) &= \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp \left[-\frac{(m_i - \bar{m}_i)^2}{2\sigma_i^2} \right] \\ p(n_j, \bar{n}_j) &= \frac{1}{\sqrt{2\pi\beta_j^2}} \exp \left[-\frac{(n_j - \bar{n}_j)^2}{2\beta_j^2} \right] \end{aligned}$$

These variances have genetic and environmental components:

$$(2.2) \quad \begin{aligned} \sigma_i^2 &= \sigma_{Gi}^2 + \sigma_{Ei}^2 \\ \beta_j^2 &= \beta_{Gj}^2 + \beta_{Ej}^2 \end{aligned}$$

Assuming predator i has a linear functional response with attack rate $a_{ij} = a_{ij}(m_i, n_j)$ on prey j , converts consumed prey j into offspring with efficiencies $e_{ij} = e_{ij}(m_i, n_j)$, and experiences a per-capita mortality rate $d_i(m_i)$, then the fitness of a predator with phenotype m_i is

$$(2.3) \quad \begin{aligned} W_i(N_1, \dots, N_u, M_i, n_1, \dots, n_v, m_i) \\ = \sum_{j=1}^v [e_{ij}(m_i, n_j) a_{ij}(m_i, n_j) N_j] - d_i(m_i) \end{aligned}$$

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

$$(2.4) \quad \begin{aligned} \bar{W}_i(N_1, \dots, N_u, M_i, \bar{n}_1, \dots, \bar{n}_v, \bar{m}_i) \\ = \int_{\mathbb{R}^{v+1}} W_i p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j \end{aligned}$$

Assume in the absence of any predators, each prey species experiences logistic-type growth with growth rates $r_j = r_j(n_j)$ and carrying capacities $K_j = K_j(n_j)$. Under

these assumptions, the fitness of a prey individual with phenotype n_j is

$$(2.5) \quad \begin{aligned} & Y_j(N_j, M_1, \dots, M_v, n_j, m_1, \dots, m_v) \\ &= r_j(n_j) \left(1 - \frac{N_j}{K_j(n_j)}\right) - \sum_{i=1}^u [a_{ij}(m_i, n_j) M_i] \end{aligned}$$

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

$$(2.6) \quad \begin{aligned} & \bar{Y}_j(N_j, M_1, \dots, M_v, \bar{n}_j, \bar{m}_1, \dots, \bar{m}_v) \\ &= \int_{\mathbb{R}^{v+1}} Y_j p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i \end{aligned}$$

The complete ditrophic model of u predator species and v prey species is given by

$$(2.7a) \quad \frac{dM_i}{dt} = M_i \bar{W}_i$$

$$(2.7b) \quad \frac{dN_j}{dt} = N_j \bar{Y}_j$$

$$(2.7c) \quad \frac{d\bar{m}_i}{dt} = \sigma_{Gi}^2 \frac{\partial \bar{W}_i}{\partial \bar{m}_i}$$

$$(2.7d) \quad \frac{d\bar{n}_j}{dt} = \beta_{Gj}^2 \frac{\partial \bar{Y}_j}{\partial \bar{n}_j}$$

where $i = 1, \dots, u$ and $j = 1, \dots, v$.

2.0.1. Model 1. This first example is a coevolutionary analog of Schreiber, Bürger, and Bolnick's apparent competition model [4]. Assume the prey growth rates and carrying capacities, r_j and K_j , and the predator death rates and efficiencies, d_i , and e_{ij} , are constant, but let an individual predator's attack rate on an individual prey, $a_{ij}(m_i, n_j)$, be maximal at an optimal trait difference, $m_i - n_j = \theta_{ij}$, and decrease away from this optimal trait difference in a Gaussian manner, i.e.,

$$(2.8) \quad a_{ij}(m_i, n_j) = \alpha_{ij} \exp \left[-\frac{((m_i - n_j) - \theta_{ij})^2}{2\tau_{ij}^2} \right]$$

where α_{ij} is the maximal attack and τ_{ij} determines how steeply the attack rate declines with distance from the optimal trait difference θ_{ij} . In effect, τ_{ij} determines how phenotypically specialized predator i must be to use prey j . Under these assumptions, the average attack rate of predator species i on prey species j is

$$(2.9) \quad \begin{aligned} \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) &= \int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \bar{m}_i) p(n_j, \bar{n}_j) dm_i dn_j \\ &= \frac{\alpha_{ij} \tau_{ij}}{\sqrt{A_{ij}}} \exp \left[-\frac{((\bar{m}_i - \bar{n}_j) - \theta_{ij})^2}{2A_{ij}} \right] \end{aligned}$$

where $A_{ij} = \tau_{ij}^2 + \sigma_i^2 + \beta_j^2$. (2.4), and (2.6) now yield explicit formulas for \bar{W}_i and \bar{Y}_j in terms of (2.9):

$$(2.10) \quad \bar{W}_i = \sum_{j=1}^v [e_{ij} \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) N_j] - d_i$$

$$(2.11) \quad \overline{Y}_j = r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u [\overline{a_{ij}}(\overline{m}_i, \overline{n}_j) M_i]$$

Relevant partial derivatives of (2.10) and (2.11) are easily computable:

$$(2.12) \quad \frac{\partial \overline{W}_i}{\partial \overline{m}_i} = \sum_{j=1}^v \left[\frac{e_{ij} N_j (\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a_{ij}}(\overline{m}_i, \overline{n}_j) \right]$$

$$(2.13) \quad \frac{\partial \overline{Y}_j}{\partial \overline{n}_j} = \sum_{i=1}^u \left[\frac{M_i (\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a_{ij}}(\overline{m}_i, \overline{n}_j) \right]$$

Thus (2.7) simplifies:

$$(2.14a) \quad \frac{dM_i}{dt} = M_i \left[\sum_{j=1}^v [e_{ij} \overline{a_{ij}}(\overline{m}_i, \overline{n}_j) N_j] - d_i \right]$$

$$(2.14b) \quad \frac{dN_j}{dt} = N_j \left[r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u [\overline{a_{ij}}(\overline{m}_i, \overline{n}_j) M_i] \right]$$

$$(2.14c) \quad \frac{d\overline{m}_i}{dt} = \sigma_{Gi}^2 \sum_{j=1}^v \left[\frac{e_{ij} N_j (\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a_{ij}}(\overline{m}_i, \overline{n}_j) \right]$$

$$(2.14d) \quad \frac{d\overline{n}_j}{dt} = \beta_{Gj}^2 \sum_{i=1}^u \left[\frac{M_i (\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a_{ij}}(\overline{m}_i, \overline{n}_j) \right]$$

2.0.2. *Model 2.* This second model introduces stabilizing selection to Model 1 by assuming each prey species has an optimal trait value by which growth rate is maximized, and decreases away from the optimal trait value in a Gaussian manner, i.e.

$$(2.15) \quad r_j(n_j) = \rho_j \exp \left[-\frac{(n_j - \phi_j)^2}{2\gamma_j^2} \right]$$

where ρ_j is the maximal growth rate of the j^{th} prey species and γ_j determines how steeply the growth rate declines with distance from the optimal trait value ϕ_j . In effect, γ_j determines how far prey j can deviate from its optimal trait value while still maintaining an adequate growth rate. Under these assumptions, the average growth rate of prey species j is

$$(2.16) \quad \begin{aligned} \overline{r_j}(\overline{n}_j) &= \int_{\mathbb{R}} r_j(n_j) p(n_j, \overline{n}_j) dn_j \\ &= \frac{\rho_j \gamma_j}{\sqrt{B_j}} \exp \left[-\frac{(\overline{n}_j - \phi_j)^2}{2B_j} \right] \end{aligned}$$

where $B_j = \beta_j^2 + \gamma_j^2$. Since \overline{W}_i is not dependent on r_j , (2.10) suffices, but \overline{Y}_j must be recalculated since it is dependent on r_j . (2.6) yields an explicit formula in terms of (2.9) and (2.16):

$$(2.17) \quad \overline{Y}_j = \overline{r_j}(\overline{n}_j) \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u [\overline{a_{ij}}(\overline{m}_i, \overline{n}_j) M_i]$$

Since \overline{W}_i did not change from Model 1, (2.14c) is sufficient for the right hand side of (2.7c). However, the right hand side of (2.7d) must be recalculated.

$$(2.18) \quad \frac{\partial \overline{Y}_j}{\partial \overline{n}_j} = \overline{r}_j(\overline{n}_j) \left(1 - \frac{N_j}{K_j}\right) \frac{\phi_j - \overline{n}_j}{B_j} + \sum_{i=1}^u \left[\frac{M_i(\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) \right]$$

Thus (2.7) simplifies:

$$(2.19a) \quad \frac{dM_i}{dt} = M_i \left[\sum_{j=1}^v [e_{ij} \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) N_j] - d_i \right]$$

$$(2.19b) \quad \frac{dN_j}{dt} = N_j \left[\overline{r}_j(\overline{n}_j) \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^u [\overline{a}_{ij}(\overline{m}_i, \overline{n}_j) M_i] \right]$$

$$(2.19c) \quad \frac{d\overline{m}_i}{dt} = \sigma_{Gi}^2 \sum_{j=1}^v \left[\frac{e_{ij} N_j (\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) \right]$$

$$(2.19d) \quad \begin{aligned} \frac{d\overline{n}_j}{dt} = & \beta_{Gj}^2 \left[\overline{r}_j(\overline{n}_j) \left(1 - \frac{N_j}{K_j}\right) \frac{\phi_j - \overline{n}_j}{B_j} \right. \\ & \left. + \sum_{i=1}^u \left[\frac{M_i(\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{A_{ij}} \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) \right] \right] \end{aligned}$$

3. RESULTS

3.1. Pairwise Predator-Prey Dynamics.

3.1.1. *Model 1.* If there is only one predator species and one prey species, then (2.14) simplifies:

$$(3.1a) \quad \frac{dM}{dt} = M [e\overline{a}(\overline{m}, \overline{n})N - d]$$

$$(3.1b) \quad \frac{dN}{dt} = N \left[r \left(1 - \frac{N}{K}\right) - \overline{a}(\overline{m}, \overline{n})M \right]$$

$$(3.1c) \quad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{eN(\theta - (\overline{m} - \overline{n}))}{A} \overline{a}(\overline{m}, \overline{n})$$

$$(3.1d) \quad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{M(\theta - (\overline{m} - \overline{n}))}{A} \overline{a}(\overline{m}, \overline{n})$$

There are three classifications of equilibria of (3.1): extinction, exclusion, and coexistence. There are an infinite amount of equilibrium points for each of these three classifications. Extinction equilibria are given by

$$(3.2) \quad (M^*, N^*, \overline{m}^*, \overline{n}^*) = (0, 0, \mu^*, \nu^*)$$

where μ^* and ν^* are arbitrary values. Exclusion equilibria are given by

$$(3.3) \quad (M^*, N^*, \overline{m}^*, \overline{n}^*) = (0, K, \mu^* + \theta, \mu^*)$$

where μ^* is an arbitrary value. Coexistence equilibria are given by

$$(3.4) \quad (M^*, N^*, \bar{m}^*, \bar{n}^*) = \left(\frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{N^*}{K} \right), \frac{d\sqrt{A}}{e\alpha\tau}, \mu^* + \theta, \mu^* \right)$$

where μ^* is an arbitrary value. Local stability analysis (Appendix II) yields that all extinction equilibria are unstable, exclusion equilibria are asymptotically stable if

$$(3.5) \quad d > \frac{Ke\alpha\tau}{\sqrt{A}}$$

and coexistence equilibria are asymptotically stable if

$$(3.6) \quad \frac{\sigma_G^2}{\beta_G^2} > \frac{r}{d} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right)$$

Intuitively, exclusion is stable if the predator death rate is high enough. Note that if (3.5) holds then (3.4) is not biologically feasible ($M^* < 0$), and so even though (3.6) would hold (since all parameters are assumed to be positive), it would be irrelevant. Since σ_G^2/β_G^2 is the ratio of predator and prey “speeds” of evolution, then intuitively, coexistence is stable if the predator is “fast” enough at evolving in comparison to the prey. If this happens, the predator trait value “catches up” to the prey trait value. Figure 1 displays a simulation that results in stable exclusion, and Figure 2 displays a simulation that results in stable coexistence.

Since (3.5) and (3.6) are not equal and opposite conditions, however, there is at least one type of non-equilibrium coexistence dynamic. Numerical simulations provide insight into these dynamics. Figure 3 depicts an evolutionary “arms race” between the predator and prey. The prey has no particular optimal value, and the predator is not fast enough at evolving to catch up to the prey, so they continuously evolve in a linear fashion. There is no stabilizing selection in this model - the prey species has no reason to stop evolving, and the predator species has no reason to stop chasing it.

3.1.2. Model 2. If there is only one predator species and one prey species, then (2.19) simplifies:

$$(3.7a) \quad \frac{dM}{dt} = M [e\bar{a}(\bar{m}, \bar{n})N - d]$$

$$(3.7b) \quad \frac{dN}{dt} = N \left[\bar{r}(\bar{n}) \left(1 - \frac{N}{K} \right) - \bar{a}(\bar{m}, \bar{n})M \right]$$

$$(3.7c) \quad \frac{d\bar{m}_i}{dt} = \sigma_G^2 \frac{eN(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n})$$

$$(3.7d) \quad \frac{d\bar{n}}{dt} = \beta_G^2 \left[\bar{r}(\bar{n}) \left(1 - \frac{N}{K} \right) \frac{\phi - \bar{n}}{B} + \frac{M(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \right]$$

Similarly to (3.1), there are three classifications of equilibrium of system (3.7): extinction, exclusion, and coexistence. There are an infinite amount of equilibrium points for the extinction and exclusion classifications, but stabilizing selection provides a unique coexistence equilibrium point. Extinction equilibria are given by

(3.2), and exclusion equilibria are given by (3.3). The coexistence equilibrium point is given by

$$(3.8) \quad (M^*, N^*, \bar{m}^*, \bar{n}^*) = \left(\frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}} \left(1 - \frac{N^*}{K} \right), \frac{d\sqrt{A}}{e\alpha\tau}, \phi + \theta, \phi \right)$$

Local stability analysis for extinction and exclusion equilibria is nearly identical to Model 1 - all extinction equilibria are unstable and exclusion equilibria are asymptotically stable if (3.5) holds. The coexistence equilibrium is asymptotically stable if

$$(3.9) \quad \frac{\sigma_G^2}{\beta_G^2} > \frac{\rho\gamma}{d\sqrt{B}} \left(1 - \frac{d\sqrt{A}}{K e \alpha \tau} \right) \left(1 - \frac{A}{B} \right)$$

Similar to Model 1, exclusion is stable if the predator death rate is high enough, and if (3.5) holds then (3.8) is not biologically feasible ($M^* < 0$), and so even though (3.9) may hold, it would be irrelevant. Again, since σ_G^2/β_G^2 is the ratio of predator and prey “speeds” of evolution, then coexistence is stable only if the predator is “fast” enough at evolving in comparison to the prey. Figure 4 displays a simulation that results in stable exclusion, and Figure 5 displays a simulation that results in stable coexistence.

(3.5) and (3.9) are not equal and opposite conditions, so there is at least one type of non-equilibrium coexistence dynamic. Numerical simulations provide insight into these dynamics. Figure 6) depicts long-term stable oscillatory dynamics. We conjecture a unique stable limit cycle exists if neither (3.5) nor (3.9) hold.

We can intuitively understand these dynamics by considering the inverse effects that the evolution of the prey trait has on its own fitness. At the same time the prey evolves its own trait value away from the predator trait value (to minimize attack rate), it must also stay close enough to its optimal trait value ϕ_j to maintain an adequate growth rate. These effects nullify each other whenever the prey trait value reaches a maximum or minimum. Immediately after the prey trait value reverses direction, the prey has double incentive to evolve toward ϕ_j : it increases its growth rate while minimizing the predator’s attack rate. Immediately after passing through ϕ_j , however, the inverse effects take hold, and the cycle begins again.

APPENDIX A: DERIVATION OF MODELS 1 AND 2

Derivation of (2.9). First note the following:

$$\begin{aligned}
& \int_{\mathbb{R}} \exp [-(ax^2 + bx + c)] = \sqrt{\frac{\pi}{a}} \exp \left[\frac{b^2}{4a} - c \right] \\
& \int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \overline{m}_i) p(n_j, \overline{n}_j) dm_i dn_j \\
&= \frac{\alpha_{ij}}{2\pi\sigma_i\beta_j} \int_{\mathbb{R}^2} \exp \left[-\frac{((m_i - n_j) - \theta_{ij})^2}{2\tau_{ij}^2} - \frac{(m_i - \overline{m}_i)^2}{2\sigma_i^2} - \frac{(n_j - \overline{n}_j)^2}{2\beta_j^2} \right] dm_i dn_j \\
&= \frac{\alpha_{ij}}{2\pi\sigma_i\beta_j} \int_{\mathbb{R}} \exp \left[-\frac{(n_j - \overline{n}_j)^2}{2\beta_j^2} \right] \int_{\mathbb{R}} \exp [-(am_i^2 + bm_i + c)] dm_i dn_j \\
& \text{where } a = \frac{\sigma_i^2 + \tau_{ij}^2}{2\sigma_i^2\tau_{ij}^2}, b = -\left(\frac{\sigma_i^2(n_j + \theta_{ij}) + \tau_{ij}^2\overline{m}_i}{\tau_{ij}^2\sigma_i^2} \right), c = \frac{\sigma_i^2(n_j + \theta_{ij})^2 + \tau_{ij}^2\overline{m}_i^2}{2\sigma_i^2\tau_{ij}^2} \\
& \implies \sqrt{\frac{\pi}{a}} \exp \left[\frac{b^2}{4a} - c \right] = \frac{\sigma_i\tau_{ij}\sqrt{2\pi}}{\sqrt{\sigma_i^2 + \tau_{ij}^2}} \exp \left[-\frac{((\overline{m}_i - n_j) - \theta_{ij})^2}{2(\sigma_i^2 + \tau_{ij}^2)} \right]
\end{aligned}$$

Thus

$$\begin{aligned}
& \int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \overline{m}_i) p(n_j, \overline{n}_j) dm_i dn_j \\
&= \frac{\alpha_{ij}\tau_{ij}}{\beta_j\sqrt{2\pi}\sqrt{\sigma_i^2 + \tau_{ij}^2}} \int_{\mathbb{R}} \exp \left[-\frac{((\overline{m}_i - n_j) - \theta_{ij})^2}{2(\sigma_i^2 + \tau_{ij}^2)} - \frac{(n_j - \overline{n}_j)^2}{2\beta_j^2} \right] dn_j \\
&= \frac{\alpha_{ij}\tau_{ij}}{\beta_j\sqrt{2\pi}\sqrt{\sigma_i^2 + \tau_{ij}^2}} \int_{\mathbb{R}} \exp [-(am_i^2 + bm_i + c)] dn_j \\
& \text{where } a = \frac{\tau_{ij}^2 + \sigma_i^2 + \beta_j^2}{2\beta_j^2(\sigma_i^2 + \tau_{ij}^2)}, b = -\frac{(\overline{m}_i - \theta_{ij})^2\beta_j^2 + (\sigma_i^2 + \tau_{ij}^2)\overline{n}_j}{\beta_j^2(\sigma_i^2 + \tau_{ij}^2)}, \text{ and } c = \frac{(\overline{m}_i - \theta_{ij})^2\beta_j^2 + \overline{n}_j^2(\sigma_i^2 + \tau_{ij}^2)}{2\beta_j^2(\sigma_i^2 + \tau_{ij}^2)} \\
& \implies \sqrt{\frac{\pi}{a}} \exp \left[\frac{b^2}{4a} - c \right] = \frac{\beta_j\sqrt{2\pi}\sqrt{\sigma_i^2 + \tau_{ij}^2}}{\sqrt{\beta_j^2 + \sigma_i^2 + \tau_{ij}^2}} \exp \left[-\frac{((\overline{m}_i - \overline{n}_j) - \theta_{ij})^2}{2(\beta_j^2 + \sigma_i^2 + \tau_{ij}^2)} \right]
\end{aligned}$$

Thus

$$\int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \overline{m}_i) p(n_j, \overline{n}_j) dm_i dn_j = \frac{\alpha_{ij}\tau_{ij}}{\sqrt{\tau_{ij}^2 + \sigma_i^2 + \beta_j^2}} \exp \left[-\frac{((\overline{m}_i - \overline{n}_j) - \theta_{ij})^2}{2(\tau_{ij}^2 + \sigma_i^2 + \beta_j^2)} \right]$$

Derivation of (2.10).

$$\overline{W}_i(N_1, \dots, N_u, M_i, \overline{n}_1, \dots, \overline{n}_v, \overline{m}_i) = \int_{\mathbb{R}^{v+1}} W_i p(m_i, \overline{m}_i) \prod_{j=1}^v p(n_j, \overline{n}_j) dm_i \prod_{j=1}^v dn_j$$

$$\begin{aligned}
&= \int_{\mathbb{R}^{v+1}} \left[\sum_{j=1}^v [e_{ij} a_{ij}(m_i, n_j) N_i] - d_i \right] p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j \\
&= \sum_{j=1}^v e_{ij} N_i \int_{\mathbb{R}^{v+1}} a_{ij}(m_i, n_j) p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j \\
&\quad - d_i \int_{\mathbb{R}^{v+1}} p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j
\end{aligned}$$

by the linearity of integrals. Since $p(m_i, \bar{m}_i)$ is independent of n_k for $k = 1, \dots, v$ and $a_{ij}(m_i, n_j)$ and $p(n_j, \bar{n}_j)$ are independent of n_k for $k = 1, \dots, n_{j-1}, n_{j+1}, \dots, n_v$, then

$$\begin{aligned}
&\int_{\mathbb{R}^{v+1}} a_{ij}(m_i, n_j) p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j \\
&= \int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \bar{m}_i) p(n_j, \bar{n}_j) \left[\int_{\mathbb{R}^{v-1}} \prod_{\substack{k=1 \\ k \neq j}}^v p(n_k, \bar{n}_k) \prod_{\substack{k=1 \\ k \neq j}}^v dn_k \right] dm_i dn_j
\end{aligned}$$

However, all traits are assumed to have normal distributions, so

$$\int_{\mathbb{R}^{v-1}} \prod_{\substack{k=1 \\ k \neq j}}^v p(n_k, \bar{n}_k) \prod_{\substack{k=1 \\ k \neq j}}^v dn_k = 1$$

Thus

$$\begin{aligned}
\int_{\mathbb{R}^{v+1}} a_{ij}(m_i, n_j) p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j &= \int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \bar{m}_i) p(n_j, \bar{n}_j) dm_i dn_j \\
&= \bar{a}_{ij}(\bar{m}_i, \bar{n}_j)
\end{aligned}$$

and

$$d_i \left(\int_{\mathbb{R}^{v+1}} p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j \right) = d_i$$

Thus,

$$\bar{W}_i(N_1, \dots, N_u, M_i, \bar{n}_1, \dots, \bar{n}_v, \bar{m}_i) = \sum_{j=1}^v [e_{ij} \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) N_i] - d_i$$

Derivation of (2.11).

$$\begin{aligned}
\bar{Y}_j(N_j, M_1, \dots, M_v, \bar{n}_j, \bar{m}_1, \dots, \bar{m}_v) &= \int_{\mathbb{R}^{u+1}} Y_j p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i \\
&= \int_{\mathbb{R}^{u+1}} \left[r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u [a_{ij}(m_i, n_j) M_i] \right] p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i
\end{aligned}$$

$$\begin{aligned}
&= r_j \left(1 - \frac{N_j}{K_j}\right) \int_{\mathbb{R}^{u+1}} p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i \\
&\quad - \sum_{i=1}^u M_i \int_{\mathbb{R}^{u+1}} a_{ij}(m_i, n_j) p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i
\end{aligned}$$

Similary to the derivation of (2.10),

$$r_j \left(1 - \frac{N_j}{K_j}\right) \left(\int_{\mathbb{R}^{u+1}} p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i \right) = r_j \left(1 - \frac{N_j}{K_j}\right)$$

and

$$\int_{\mathbb{R}^{u+1}} a_{ij}(m_i, n_j) p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i = \bar{a}_{ij}(\bar{m}_i, \bar{n}_j)$$

Thus,

$$\bar{Y}_j(N_j, M_1, \dots, M_v, \bar{n}_j, \bar{m}_1, \dots, \bar{m}_v) = r_j \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^u [\bar{a}_{ij}(\bar{m}_i, \bar{n}_j) M_i]$$

Derivation of (2.16).

$$\begin{aligned}
\bar{r}_j(\bar{n}_j) &= \int_{\mathbb{R}} r_j(n_j) p(n_j, \bar{n}_j) dn_j \\
&= \int_{\mathbb{R}} \left(\rho_j \exp \left[-\frac{(n_j - \phi_j)^2}{2\gamma_j^2} \right] \right) \left(\frac{1}{\sqrt{2\pi\beta_j^2}} \exp \left[-\frac{(n_j - \bar{n}_j)^2}{2\beta_j^2} \right] \right) dn_j \\
&= \frac{\rho_j}{\beta_j \sqrt{2\pi}} \int_{\mathbb{R}} \exp [-(an_j^2 + bn_j + c)] dn_j
\end{aligned}$$

$$\text{where } a = \frac{\beta_j^2 + \gamma_j^2}{2\beta_j^2\gamma_j^2}, b = -\left(\frac{\phi_j\beta_j^2 + \bar{n}_j\gamma_j^2}{\beta_j^2\gamma_j^2} \right), \text{ and } c = \frac{\phi_j^2\beta_j^2 + \bar{n}_j^2\gamma_j^2}{2\beta_j^2\gamma_j^2}$$

$$\begin{aligned}
\Rightarrow \sqrt{\frac{\pi}{a}} \exp \left[\frac{b^2}{4a} - c \right] &= \frac{\beta_j\gamma_j\sqrt{2\pi}}{\sqrt{\beta_j^2 + \gamma_j^2}} \exp \left[-\frac{(\bar{n}_j - \phi_j)^2}{2(\beta_j^2 + \gamma_j^2)} \right] \\
\Rightarrow \bar{r}_j(n_j) &= \frac{\rho_j\gamma_j}{\sqrt{B_j}} \exp \left[-\frac{(\bar{n}_j - \phi_j)^2}{2B_j} \right]
\end{aligned}$$

Derivation of (2.17).

$$\begin{aligned}
\bar{Y}_j(N_j, M_1, \dots, M_v, \bar{n}_j, \bar{m}_1, \dots, \bar{m}_v) &= \int_{\mathbb{R}^{u+1}} Y_j p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i \\
&= \int_{\mathbb{R}^{u+1}} \left[r_j(n_j) \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^u [a_{ij}(m_i, n_j) M_i] \right] p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i
\end{aligned}$$

$$\begin{aligned}
&= \left(1 - \frac{N_j}{K_j}\right) \int_{\mathbb{R}^{u+1}} r_j(n_j) p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i \\
&\quad - \sum_{i=1}^u M_i \int_{\mathbb{R}^{u+1}} a_{ij}(m_i, n_j) p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i
\end{aligned}$$

Similarity to the derivation of (2.10), since $r_j(n_j)$ and $p(n_j, \bar{n}_j)$ are not dependent on n_k for $k = 1, \dots, j-1, j+1, \dots, v$, then

$$\begin{aligned}
&\int_{\mathbb{R}^{u+1}} r_j(n_j) p(m_i, \bar{m}_i) \prod_{j=1}^v p(n_j, \bar{n}_j) dm_i \prod_{j=1}^v dn_j \\
&= \int_{\mathbb{R}} r_j(n_j) p(n_j, \bar{n}_j) \left[\int_{\mathbb{R}^u} p(m_i, \bar{m}_i) \prod_{\substack{k=1 \\ k \neq j}}^v p(n_k, \bar{n}_k) dm_i \prod_{\substack{k=1 \\ k \neq j}}^v dn_k \right] dn_j \\
&= \int_{\mathbb{R}} r_j(n_j) p(n_j, \bar{n}_j) dn_j \\
&= \bar{r}_j(\bar{n}_j)
\end{aligned}$$

and

$$\int_{\mathbb{R}^{u+1}} a_{ij}(m_i, n_j) p(n_j, \bar{n}_j) \prod_{i=1}^u p(m_i, \bar{m}_i) dn_j \prod_{i=1}^u dm_i = \bar{a}_{ij}(\bar{m}_i, \bar{n}_j)$$

Thus,

$$\bar{Y}_j(N_j, M_1, \dots, M_v, \bar{n}_j, \bar{m}_1, \dots, \bar{m}_v) = \bar{r}_j(\bar{n}_j) \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^u [\bar{a}_{ij}(\bar{m}_i, \bar{n}_j) M_i]$$

APPENDIX B: EQUILIBRIA AND LOCAL STABILITY ANALYSIS OF (3.1)

$$\begin{aligned}
f_1 &= \frac{dM}{dt} = M [e\bar{a}(\bar{m}, \bar{n})N - d] \\
f_2 &= \frac{dN}{dt} = N \left[r \left(1 - \frac{N}{K} \right) - \bar{a}(\bar{m}, \bar{n})M \right] \\
f_3 &= \frac{d\bar{m}}{dt} = \sigma_G^2 \frac{eN(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \\
f_4 &= \frac{d\bar{n}}{dt} = \beta_G^2 \frac{M(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n})
\end{aligned}$$

$$\begin{aligned}
f_1 = 0 &\implies M = 0 \quad \text{or} \quad N = \frac{d}{e\bar{a}(\bar{m}, \bar{n})} \\
f_2 = 0 &\implies N = 0 \quad \text{or} \quad M = \frac{r}{\bar{a}(\bar{m}, \bar{n})} \left(1 - \frac{N}{K} \right) \\
f_3 = 0 &\implies N = 0 \quad \text{or} \quad \bar{m} - \bar{n} = \theta \\
f_4 = 0 &\implies M = 0 \quad \text{or} \quad \bar{m} - \bar{n} = \theta
\end{aligned}$$

Clearly, $M = N = 0$ satisfies equilibrium, and \bar{m} and \bar{n} are arbitrary. This gives the extinction equilibria. Suppose $M = 0$ but $N \neq 0$. Then $f_2 = 0 \implies N = K$ and $f_3 = 0 \implies \bar{m} - \bar{n} = \theta$. This gives the exclusion equilibria. Supposing $M \neq 0$ and $N \neq 0$, then $f_3 = f_4 = 0 \implies \bar{m} - \bar{n} = \theta \implies \bar{a}(\bar{m}, \bar{n}) = \frac{\alpha\tau}{\sqrt{A}} \implies N = \frac{d\sqrt{A}}{e\alpha\tau} \implies M = \frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{\sqrt{A}}{Ke\alpha\tau} \right)$. By exhaustion, this gives the only other set of equilibria: the coexistence equilibria.

To solve for local stability conditions, we find the eigenvalues of the community matrix evaluated at each equilibrium point. First, note the partial derivatives of f_1 , f_2 , f_3 , and f_4 :

$$\begin{aligned}
\frac{\partial f_1}{\partial M} &= e\bar{a}(\bar{m}, \bar{n})N - d \\
\frac{\partial f_1}{\partial N} &= Me\bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_1}{\partial \bar{m}} &= \frac{MN e(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_1}{\partial \bar{n}} &= \frac{MN e((\bar{m} - \bar{n}) - \theta)}{A} \bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_2}{\partial M} &= -N\bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_2}{\partial N} &= r \left(1 - \frac{2N}{K} \right) - M\bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_2}{\partial \bar{m}} &= -\frac{MN(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n})
\end{aligned}$$

$$\begin{aligned}
\frac{\partial f_2}{\partial n} &= -\frac{MN((\bar{m} - \bar{n}) - \theta)}{A} \bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_3}{\partial M} &= 0 \\
\frac{\partial f_3}{\partial N} &= \frac{\sigma_G^2 e}{A} \bar{a}(\bar{m}, \bar{n}) (\theta - (\bar{m} - \bar{n})) \\
\frac{\partial f_3}{\partial \bar{m}} &= \frac{\sigma_G^2 e N}{A} \bar{a}(\bar{m}, \bar{n}) \left(\frac{(\theta - (\bar{m} - \bar{n}))^2}{A} - 1 \right) \\
\frac{\partial f_3}{\partial \bar{n}} &= \frac{\sigma_G^2 e N}{A} \bar{a}(\bar{m}, \bar{n}) \left(1 - \frac{(\theta - (\bar{m} - \bar{n}))^2}{A} \right) \\
\frac{\partial f_4}{\partial M} &= \frac{\beta_G^2}{A} \bar{a}(\bar{m}, \bar{n}) (\theta - (\bar{m} - \bar{n})) \\
\frac{\partial f_4}{\partial N} &= 0 \\
\frac{\partial f_4}{\partial \bar{m}} &= \frac{\beta_G^2 M}{A} \bar{a}(\bar{m}, \bar{n}) \left(\frac{(\theta - (\bar{m} - \bar{n}))^2}{A} - 1 \right) \\
\frac{\partial f_4}{\partial \bar{n}} &= \frac{\beta_G^2 M}{A} \bar{a}(\bar{m}, \bar{n}) \left(1 - \frac{(\theta - (\bar{m} - \bar{n}))^2}{A} \right)
\end{aligned}$$

Let the extinction, exclusion, and coexistence equilibrium be denoted as

$$\begin{aligned}
E_{\text{ext}} &= (M^*, N^*, \bar{m}^*, \bar{n}^*) = (0, 0, \mu^*, \nu^*) \\
E_{\text{excl}} &= (M^*, N^*, \bar{m}^*, \bar{n}^*) = (0, K, \mu^* + \theta, \mu^*) \\
E_{\text{coex}} &= (M^*, N^*, \bar{m}^*, \bar{n}^*) = \left(\frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{N^*}{K} \right), \frac{d\sqrt{A}}{e\alpha\tau}, \mu^* + \theta, \mu^* \right)
\end{aligned}$$

Then denote $J^*|_{E_{\text{ext}}}$, $J^*|_{E_{\text{excl}}}$, and $J^*|_{E_{\text{coex}}}$ as the community matrices evaluated at those points.

$$\begin{aligned}
J^*|_{E_{\text{ext}}} &= \begin{pmatrix} \frac{\partial f_1}{\partial M}|_{E_{\text{ext}}} & \frac{\partial f_1}{\partial N}|_{E_{\text{ext}}} & \frac{\partial f_1}{\partial \bar{m}}|_{E_{\text{ext}}} & \frac{\partial f_1}{\partial \bar{n}}|_{E_{\text{ext}}} \\ \frac{\partial f_2}{\partial M}|_{E_{\text{ext}}} & \frac{\partial f_2}{\partial N}|_{E_{\text{ext}}} & \frac{\partial f_2}{\partial \bar{m}}|_{E_{\text{ext}}} & \frac{\partial f_2}{\partial \bar{n}}|_{E_{\text{ext}}} \\ \frac{\partial f_3}{\partial M}|_{E_{\text{ext}}} & \frac{\partial f_3}{\partial N}|_{E_{\text{ext}}} & \frac{\partial f_3}{\partial \bar{m}}|_{E_{\text{ext}}} & \frac{\partial f_3}{\partial \bar{n}}|_{E_{\text{ext}}} \\ \frac{\partial f_4}{\partial M}|_{E_{\text{ext}}} & \frac{\partial f_4}{\partial N}|_{E_{\text{ext}}} & \frac{\partial f_4}{\partial \bar{m}}|_{E_{\text{ext}}} & \frac{\partial f_4}{\partial \bar{n}}|_{E_{\text{ext}}} \end{pmatrix} \\
&= \begin{pmatrix} -d & 0 & 0 & 0 \\ 0 & r & 0 & 0 \\ 0 & \frac{\sigma_G^2 e (\theta - (\mu^* - \nu^*))}{A} \bar{a}(\mu^*, \nu^*) & 0 & 0 \\ \frac{\beta_G^2 (\theta - (\mu^* - \nu^*))}{A} \bar{a}(\mu^*, \nu^*) & 0 & 0 & 0 \end{pmatrix}
\end{aligned}$$

This is an upper-triangular matrix, and thus the eigenvalues are the entries on the main diagonal: $-d$, r , and 0 . Since one of the eigenvalues, namely r , is positive,

the E_{ext} is locally unstable.

$$\begin{aligned}
 J^*|_{E_{\text{excl}}} &= \begin{pmatrix} \frac{\partial f_1}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_1}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_1}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_1}{\partial \bar{n}}|_{E_{\text{excl}}} \\ \frac{\partial f_2}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_2}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_2}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_2}{\partial \bar{n}}|_{E_{\text{excl}}} \\ \frac{\partial f_3}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_3}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_3}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_3}{\partial \bar{n}}|_{E_{\text{excl}}} \\ \frac{\partial f_4}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_4}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_4}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_4}{\partial \bar{n}}|_{E_{\text{excl}}} \end{pmatrix} \\
 &= \begin{pmatrix} \frac{Ke\alpha\tau}{\sqrt{A}} - d & 0 & 0 & 0 \\ -\frac{K\alpha\tau}{\sqrt{A}} & -r & 0 & 0 \\ 0 & 0 & -\frac{\sigma_G^2 Ke\alpha\tau}{A^{3/2}} & \frac{\sigma_G^2 Ke\alpha\tau}{A^{3/2}} \\ 0 & 0 & 0 & 0 \end{pmatrix}
 \end{aligned}$$

The eigenvalues are $\frac{Ke\alpha\tau}{\sqrt{A}} - d$, $-r$ and $-\frac{\sigma_G^2 Ke\alpha\tau}{A^{3/2}}$, 0 . (The eigenvalues are easily computable by swapping the third and fourth rows and columns to obtain an upper-triangular matrix). All of these are non-positive if (3.5) holds.

$$\begin{aligned}
 J^*|_{E_{\text{coex}}} &= \begin{pmatrix} \frac{\partial f_1}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_1}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_1}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_1}{\partial \bar{n}}|_{E_{\text{coex}}} \\ \frac{\partial f_2}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_2}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_2}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_2}{\partial \bar{n}}|_{E_{\text{coex}}} \\ \frac{\partial f_3}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_3}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_3}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_3}{\partial \bar{n}}|_{E_{\text{coex}}} \\ \frac{\partial f_4}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_4}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_4}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_4}{\partial \bar{n}}|_{E_{\text{coex}}} \end{pmatrix} \\
 &= \begin{pmatrix} 0 & er\left(1 - \frac{N^*}{K}\right) & 0 & 0 \\ -\frac{d}{e} & -\frac{rN^*}{K} & 0 & 0 \\ 0 & 0 & -\frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ 0 & 0 & -\frac{\beta_G^2 r}{A}\left(1 - \frac{N^*}{K}\right) & \frac{\beta_G^2 r}{A}\left(1 - \frac{N^*}{K}\right) \end{pmatrix}
 \end{aligned}$$

This is a block diagonal matrix, and so the eigenvalues can be calculated by finding the eigenvalues of each block.

$$J_1 = \begin{pmatrix} 0 & er\left(1 - \frac{N^*}{K}\right) \\ -\frac{d}{e} & -\frac{rN^*}{K} \end{pmatrix} \quad \text{and} \quad J_2 = \begin{pmatrix} -\frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ -\frac{\beta_G^2 r}{A}\left(1 - \frac{N^*}{K}\right) & \frac{\beta_G^2 r}{A}\left(1 - \frac{N^*}{K}\right) \end{pmatrix}$$

The eigenvalues of J_1 are

$$\lambda_{1,2} = \frac{1}{2} \left[-\frac{rN^*}{K} \pm \sqrt{\left(\frac{rN^*}{K}\right)^2 - 4rd\left(1 - \frac{N^*}{K}\right)} \right]$$

Since $N^* < K$, $\sqrt{\left(\frac{rN^*}{K}\right)^2 - 4rd\left(1 - \frac{N^*}{K}\right)} < \left|\frac{rN^*}{K}\right|$, and thus $\text{Re}(\lambda_{1,2}) < 0$.

The eigenvalues of J_2 are

$$\lambda_{3,4} = \frac{1}{2} \left[- \left(\frac{d\sigma_G^2 - r\beta_G^2 \left(1 - \frac{N^*}{K} \right)}{A} \right) \pm \sqrt{\Delta} \right]$$

where

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

Again, since $N^* < K$, $\sqrt{\Delta} < \left| \frac{d\sigma_G^2 - r\beta_G^2 \left(1 - \frac{N^*}{K} \right)}{A} \right|$, and thus $\text{Re}(\lambda_{3,4}) < 0$ if and only if (3.6) holds.

APPENDIX C: EQUILIBRIA AND LOCAL STABILITY ANALYSIS OF (3.7)

$$\begin{aligned}
f_1 &= \frac{dM}{dt} = M[e\bar{a}(\bar{m}, \bar{n})N - d] \\
f_2 &= \frac{dN}{dt} = N\left[\bar{r}(\bar{n})\left(1 - \frac{N}{K}\right) - \bar{a}(\bar{m}, \bar{n})M\right] \\
f_3 &= \frac{d\bar{m}}{dt} = \sigma_G^2 \frac{eN(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \\
f_4 &= \frac{d\bar{n}}{dt} = \beta_G^2 \left[\bar{r}(\bar{n})\left(1 - \frac{N}{K}\right) \frac{\phi - \bar{n}}{B} + \frac{M(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \right]
\end{aligned}$$

$$\begin{aligned}
f_1 = 0 &\implies M = 0 && \text{or} && N &= \frac{d}{e\bar{a}(\bar{m}, \bar{n})} \\
f_2 = 0 &\implies N = 0 && \text{or} && M &= \frac{\bar{r}(\bar{n})}{\bar{a}(\bar{m}, \bar{n})} \left(1 - \frac{N}{K}\right) \\
f_3 = 0 &\implies N = 0 && \text{or} && \bar{m} - \bar{n} &= \theta \\
f_4 = 0 &\implies M = 0 && \text{or} && \bar{r}(\bar{n})\left(1 - \frac{N}{K}\right) \frac{\phi - \bar{n}}{B} &= \frac{M((\bar{m} - \bar{n}) - \theta)}{A} \bar{a}(\bar{m}, \bar{n})
\end{aligned}$$

Clearly, $M = N = 0$ satisfies equilibrium, and \bar{m} and \bar{n} are arbitrary. This gives the extinction equilibria. Suppose $M = 0$ but $N \neq 0$. Then $f_2 = 0 \implies N = K$ and $f_3 = 0 \implies \bar{m} - \bar{n} = \theta$. This gives the exclusion equilibria. Supposing $M \neq 0$ and $N \neq 0$, then $f_3 = 0 \implies \bar{m} - \bar{n} = \theta \implies \bar{a}(\bar{m}, \bar{n}) = \frac{\alpha\tau}{\sqrt{A}} \implies N = \frac{d\sqrt{A}}{e\alpha\tau}$. Since $\bar{m} - \bar{n} = \theta$, then $f_4 = 0 \implies \bar{n} = \phi$ or $N = K$. But if $N = K$, then $f_2 = 0 \implies M = 0$, a contradiction. Thus $\bar{n} = \phi$, which implies $\bar{m} = \phi + \theta$ and $M = \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}} \left(1 - \frac{\sqrt{A}}{Ke\alpha\tau}\right)$. By exhaustion, this gives the only other equilibrium: the coexistence equilibrium point.

To solve for local stability conditions, we find the eigenvalues of the community matrix evaluated at each equilibrium point. First, note the partial derivatives of f_1 , f_2 , f_3 , and f_4 :

$$\begin{aligned}
\frac{\partial f_1}{\partial M} &= e\bar{a}(\bar{m}, \bar{n})N - d \\
\frac{\partial f_1}{\partial N} &= Me\bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_1}{\partial \bar{m}} &= \frac{MNe(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_1}{\partial \bar{n}} &= \frac{MNe((\bar{m} - \bar{n}) - \theta)}{A} \bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_2}{\partial M} &= -N\bar{a}(\bar{m}, \bar{n}) \\
\frac{\partial f_2}{\partial N} &= \bar{r}(\bar{n}) \left(1 - \frac{2N}{K}\right) - M\bar{a}(\bar{m}, \bar{n})
\end{aligned}$$

$$\begin{aligned}\frac{\partial f_2}{\partial \bar{m}} &= -\frac{MN(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \\ \frac{\partial f_2}{\partial \bar{n}} &= N \left[\bar{r}(\bar{n}) \left(1 - \frac{N}{K} \right) \frac{\phi - \bar{n}}{B} - \frac{M((\bar{m} - \bar{n}) - \theta)}{A} \bar{a}(\bar{m}, \bar{n}) \right]\end{aligned}$$

$$\begin{aligned}\frac{\partial f_3}{\partial M} &= 0 \\ \frac{\partial f_3}{\partial N} &= \frac{\sigma_G^2 e}{A} \bar{a}(\bar{m}, \bar{n}) (\theta - (\bar{m} - \bar{n})) \\ \frac{\partial f_3}{\partial \bar{m}} &= \frac{\sigma_G^2 e N}{A} \bar{a}(\bar{m}, \bar{n}) \left(\frac{(\theta - (\bar{m} - \bar{n}))^2}{A} - 1 \right) \\ \frac{\partial f_3}{\partial \bar{n}} &= \frac{\sigma_G^2 e N}{A} \bar{a}(\bar{m}, \bar{n}) \left(1 - \frac{(\theta - (\bar{m} - \bar{n}))^2}{A} \right)\end{aligned}$$

$$\begin{aligned}\frac{\partial f_4}{\partial M} &= \frac{\beta_G^2}{A} \bar{a}(\bar{m}, \bar{n}) (\theta - (\bar{m} - \bar{n})) \\ \frac{\partial f_4}{\partial N} &= -\frac{\beta_G^2 \bar{r}(\bar{n})}{K} \cdot \frac{\phi - \bar{n}}{B} \\ \frac{\partial f_4}{\partial \bar{m}} &= \frac{\beta_G^2 M}{A} \bar{a}(\bar{m}, \bar{n}) \left(\frac{(\theta - (\bar{m} - \bar{n}))^2}{A} - 1 \right) \\ \frac{\partial f_4}{\partial \bar{n}} &= \beta_G^2 \left[\frac{\bar{r}(\bar{n})}{B} \left(1 - \frac{N}{K} \right) \left(\frac{(\phi - \bar{n})^2}{B} - 1 \right) + \frac{M}{A} \bar{a}(\bar{m}, \bar{n}) \left(1 - \frac{(\theta - (\bar{m} - \bar{n}))^2}{A} \right) \right]\end{aligned}$$

Let the extinction, exclusion, and coexistence equilibria be denoted as

$$\begin{aligned}E_{\text{ext}} &= (M^*, N^*, \bar{m}^*, \bar{n}^*) = (0, 0, \mu^*, \nu^*) \\ E_{\text{excl}} &= (M^*, N^*, \bar{m}^*, \bar{n}^*) = (0, K, \mu^* + \theta, \mu^*) \\ E_{\text{coex}} &= (M^*, N^*, \bar{m}^*, \bar{n}^*) = \left(\frac{\rho \gamma \sqrt{A}}{\alpha \tau \sqrt{B}} \left(1 - \frac{N^*}{K} \right), \frac{d \sqrt{A}}{e \alpha \tau}, \phi + \theta, \phi \right)\end{aligned}$$

Then denote $J^*|_{E_{\text{ext}}}$, $J^*|_{E_{\text{excl}}}$, and $J^*|_{E_{\text{coex}}}$ as the community matrices evaluated at those points.

$$J^*|_{E_{\text{ext}}} = \begin{pmatrix} \frac{\partial f_1}{\partial M} \Big|_{E_{\text{ext}}} & \frac{\partial f_1}{\partial N} \Big|_{E_{\text{ext}}} & \frac{\partial f_1}{\partial \bar{m}} \Big|_{E_{\text{ext}}} & \frac{\partial f_1}{\partial \bar{n}} \Big|_{E_{\text{ext}}} \\ \frac{\partial f_2}{\partial M} \Big|_{E_{\text{ext}}} & \frac{\partial f_2}{\partial N} \Big|_{E_{\text{ext}}} & \frac{\partial f_2}{\partial \bar{m}} \Big|_{E_{\text{ext}}} & \frac{\partial f_2}{\partial \bar{n}} \Big|_{E_{\text{ext}}} \\ \frac{\partial f_3}{\partial M} \Big|_{E_{\text{ext}}} & \frac{\partial f_3}{\partial N} \Big|_{E_{\text{ext}}} & \frac{\partial f_3}{\partial \bar{m}} \Big|_{E_{\text{ext}}} & \frac{\partial f_3}{\partial \bar{n}} \Big|_{E_{\text{ext}}} \\ \frac{\partial f_4}{\partial M} \Big|_{E_{\text{ext}}} & \frac{\partial f_4}{\partial N} \Big|_{E_{\text{ext}}} & \frac{\partial f_4}{\partial \bar{m}} \Big|_{E_{\text{ext}}} & \frac{\partial f_4}{\partial \bar{n}} \Big|_{E_{\text{ext}}} \end{pmatrix}$$

$$= \begin{pmatrix} -d & 0 & 0 & 0 \\ 0 & \frac{\rho\gamma}{\sqrt{B}} & 0 & 0 \\ 0 & \frac{\sigma_G^2 e(\theta - (\mu^* - \nu^*)) \bar{a}(\mu^*, \nu^*)}{A} & 0 & 0 \\ \frac{\beta_G^2 (\theta - (\mu^* - \nu^*)) \bar{a}(\mu^*, \nu^*)}{A} & -\frac{\beta_G^2 \bar{r}(\nu^*)}{K} \cdot \frac{\phi - \nu^*}{B} & 0 & \beta_G^2 \frac{\bar{r}(\bar{n})}{B} \left(\frac{(\phi - \bar{n})^2}{B} - 1 \right) \end{pmatrix}$$

This is an upper-triangular matrix, and thus the eigenvalues are the entries on the main diagonal: $-d$, $\frac{\rho\gamma}{\sqrt{B}}$, 0, and $\beta_G^2 \frac{\bar{r}(\bar{n})}{B} \left(\frac{(\phi - \bar{n})^2}{B} - 1 \right)$. Since one of the eigenvalues, namely $\frac{\rho\gamma}{\sqrt{B}}$, is positive, the E_{ext} is locally unstable.

$$J^*|_{E_{\text{excl}}} = \begin{pmatrix} \frac{\partial f_1}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_1}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_1}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_1}{\partial \bar{n}}|_{E_{\text{excl}}} \\ \frac{\partial f_2}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_2}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_2}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_2}{\partial \bar{n}}|_{E_{\text{excl}}} \\ \frac{\partial f_3}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_3}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_3}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_3}{\partial \bar{n}}|_{E_{\text{excl}}} \\ \frac{\partial f_4}{\partial M}|_{E_{\text{excl}}} & \frac{\partial f_4}{\partial N}|_{E_{\text{excl}}} & \frac{\partial f_4}{\partial \bar{m}}|_{E_{\text{excl}}} & \frac{\partial f_4}{\partial \bar{n}}|_{E_{\text{excl}}} \end{pmatrix}$$

$$= \begin{pmatrix} \frac{Ke\alpha\tau}{\sqrt{A}} - d & 0 & 0 & 0 \\ -\frac{Ke\alpha\tau}{\sqrt{A}} & -\frac{\rho\gamma}{\sqrt{B}} & 0 & 0 \\ 0 & 0 & -\frac{\sigma_G^2 Ke\alpha\tau}{A^{3/2}} & \frac{\sigma_G^2 Ke\alpha\tau}{A^{3/2}} \\ 0 & -\frac{\beta_G^2 \rho\gamma}{K\sqrt{B}} \cdot \frac{\phi - \mu^*}{B} & 0 & 0 \end{pmatrix}$$

The eigenvalues are $\frac{Ke\alpha\tau}{\sqrt{A}} - d$, $-\frac{\rho\gamma}{\sqrt{B}}$ and $-\frac{\sigma_G^2 Ke\alpha\tau}{A^{3/2}}$, 0. (The eigenvalues are easily computable by swapping the third and fourth rows and columns to obtain an upper-triangular matrix). All of these are non-positive if (3.5) holds.

$$J^*|_{E_{\text{coex}}} = \begin{pmatrix} \frac{\partial f_1}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_1}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_1}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_1}{\partial \bar{n}}|_{E_{\text{coex}}} \\ \frac{\partial f_2}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_2}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_2}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_2}{\partial \bar{n}}|_{E_{\text{coex}}} \\ \frac{\partial f_3}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_3}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_3}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_3}{\partial \bar{n}}|_{E_{\text{coex}}} \\ \frac{\partial f_4}{\partial M}|_{E_{\text{coex}}} & \frac{\partial f_4}{\partial N}|_{E_{\text{coex}}} & \frac{\partial f_4}{\partial \bar{m}}|_{E_{\text{coex}}} & \frac{\partial f_4}{\partial \bar{n}}|_{E_{\text{coex}}} \end{pmatrix}$$

$$= \begin{pmatrix} 0 & \frac{e\rho\gamma}{\sqrt{B}} \left(1 - \frac{N^*}{K}\right) & 0 & 0 \\ -\frac{d}{e} & -\frac{\rho\gamma N^*}{K\sqrt{B}} & 0 & 0 \\ 0 & 0 & -\frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ 0 & 0 & -\frac{\beta_G^2 \rho\gamma}{A\sqrt{B}} \left(1 - \frac{N^*}{K}\right) & \frac{\beta_G^2 \rho\gamma}{\sqrt{B}} \left(1 - \frac{N^*}{K}\right) \left(\frac{1}{A} - \frac{1}{B}\right) \end{pmatrix}$$

This is a block diagonal matrix, and so the eigenvalues can be calculated by finding the eigenvalues of each block.

$$J_1 = \begin{pmatrix} 0 & \frac{e\rho\gamma}{\sqrt{B}} \left(1 - \frac{N^*}{K}\right) \\ -\frac{d}{e} & -\frac{\rho\gamma N^*}{K\sqrt{B}} \end{pmatrix} \quad \text{and} \quad J_2 = \begin{pmatrix} -\frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ -\frac{\beta_G^2 \rho\gamma}{A\sqrt{B}} \left(1 - \frac{N^*}{K}\right) & \frac{\beta_G^2 \rho\gamma}{\sqrt{B}} \left(1 - \frac{N^*}{K}\right) \left(\frac{1}{A} - \frac{1}{B}\right) \end{pmatrix}$$

The eigenvalues of J_1 are

$$\lambda_{1,2} = \frac{1}{2} \left[-\frac{\rho\gamma N^*}{K\sqrt{B}} \pm \sqrt{\left(\frac{\rho\gamma N^*}{K\sqrt{B}}\right)^2 - 4\rho\gamma d \left(1 - \frac{N^*}{K}\right)} \right]$$

Since $N^* < K$, $\sqrt{\left(\frac{\rho\gamma N^*}{K\sqrt{B}}\right)^2 - 4\rho\gamma d \left(1 - \frac{N^*}{K}\right)} < \left|\frac{\rho\gamma N^*}{K\sqrt{B}}\right|$, and thus $\text{Re}(\lambda_{1,2}) < 0$.

For simplicity, let

$$C = \frac{d\sigma_G^2}{A}$$

and $D = \frac{\beta_G^2 \rho\gamma}{\sqrt{B}} \left(1 - \frac{N^*}{K}\right)$

then the eigenvalues of J_2 are

$$\lambda_{3,4} = \frac{1}{2} \left[-\left(C + D \left[\frac{1}{B} - \frac{1}{A}\right]\right) \pm \sqrt{\left(C + D \left[\frac{1}{B} - \frac{1}{A}\right]\right)^2 - \left(\frac{4CD}{B}\right)} \right]$$

Again, $N^* < K \implies D > 0 \implies \sqrt{\left(C + D \left[\frac{1}{B} - \frac{1}{A}\right]\right)^2 - \left(\frac{4CD}{B}\right)} < \left|C + D \left[\frac{1}{B} - \frac{1}{A}\right]\right|$, and thus $\text{Re}(\lambda_{3,4}) < 0$ if and only if (3.9) holds.

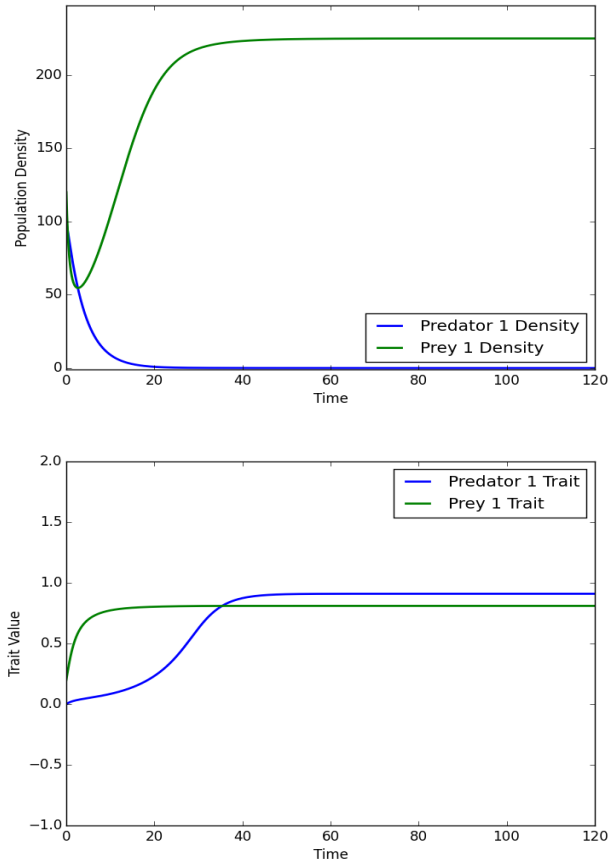


FIGURE 1. Model 1: Exclusion Equilibrium

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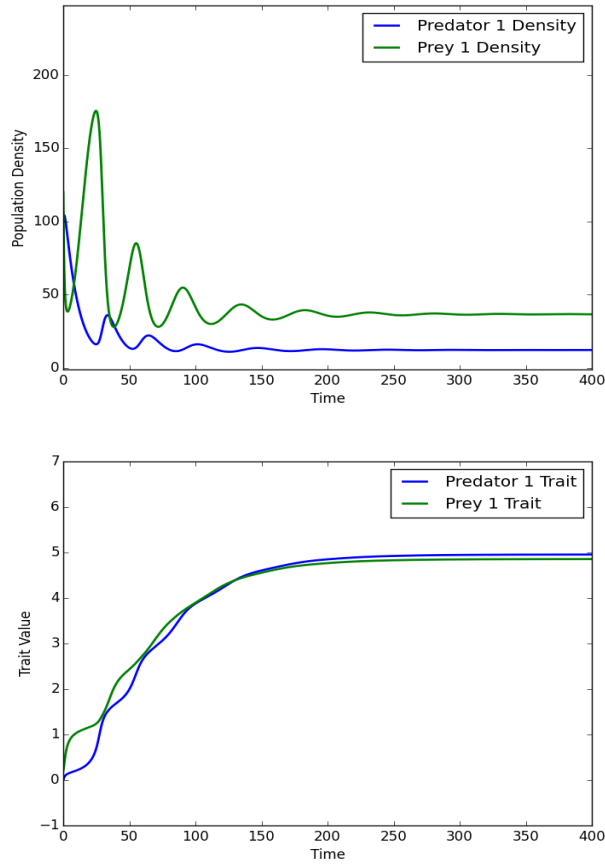


FIGURE 2. Model 1: Coexistence Equilibrium

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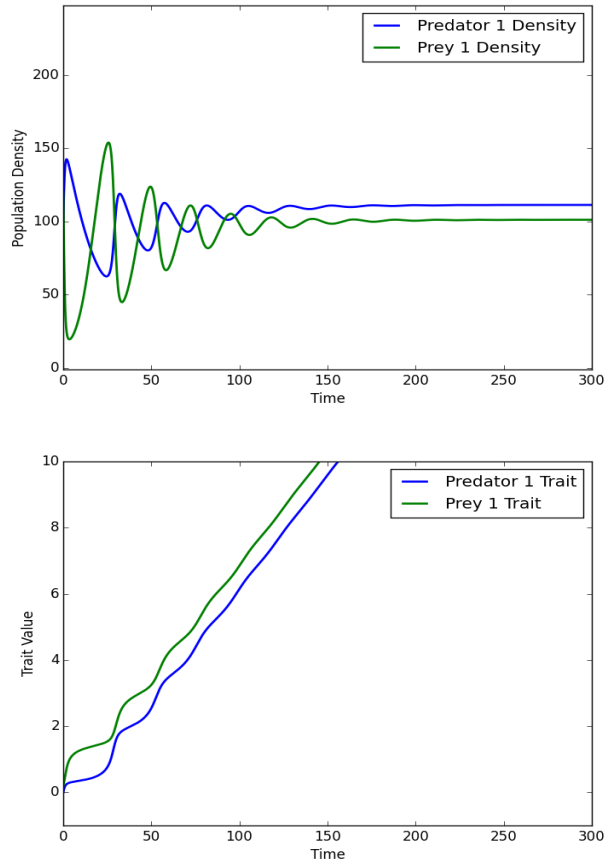


FIGURE 3. Model 1: Non-Equilibrium Coexistence

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DEPARTMENT OF MATHEMATICS, CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

E-mail address: samuel.fleischer.746@my.csun.edu, pablo.chavarria.189@my.csun.edu

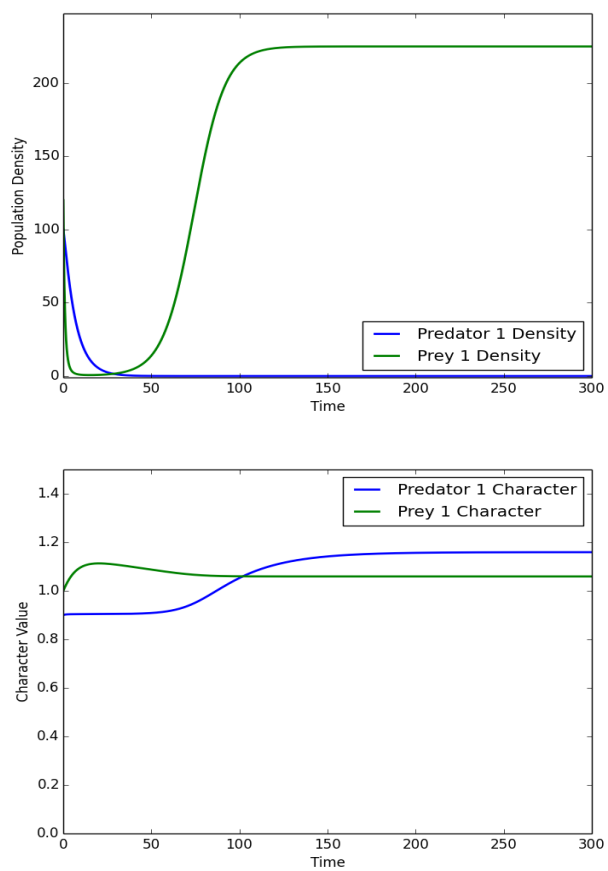


FIGURE 4. Model 2: Exclusion Equilibrium

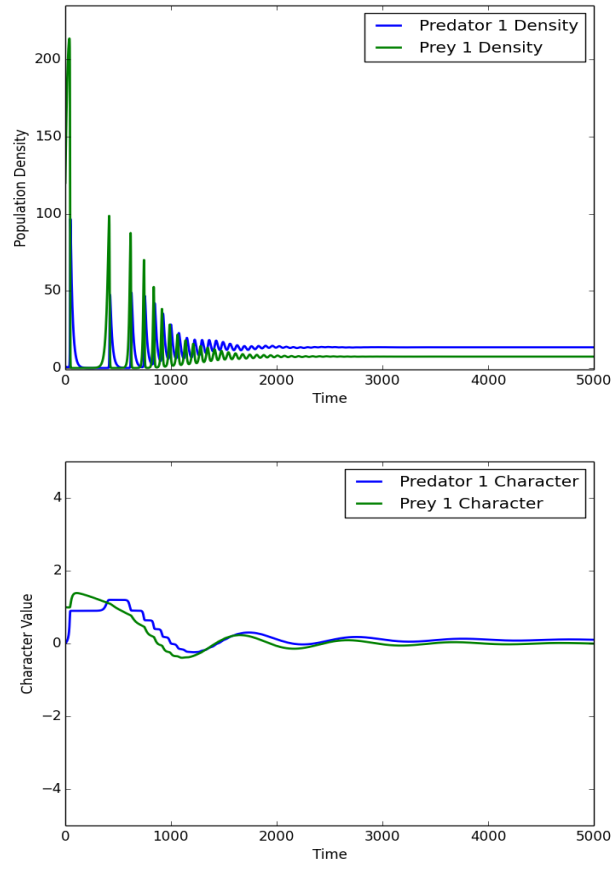


FIGURE 5. Model 2: Coexistence Equilibrium

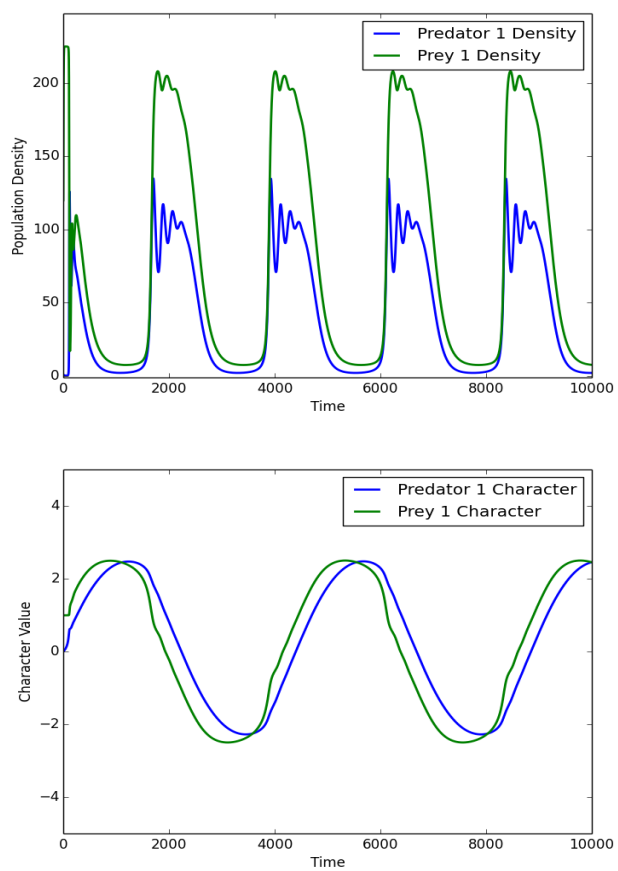


FIGURE 6. Model 2: Non-Equilibrium, Cyclic Coexistence