

# The Effects of Intraspecific Genetic Variation on the Dynamics of Predator-Prey Ecological Communities

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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 propose a coevolutionary ditrophic model and provide realistic ecologic parameters that produce all dynamics.

## Introduction

Natural populations differ in size, morphology, physiology, and behavior. This genetic variation is a central and organizing theme of evolutionary biology [1].

## Model and Methods

We consider the ditrophic dynamics of  $v$  predator populations with densities  $M_i = M_i(t)$ , consuming  $u$  prey populations with densities  $N_j = N_j(t)$ , respectively ( $i = 1, \dots, v$ , and  $j = 1, \dots, u$ ). Ecological parameters will be defined as functions of predator phenotypic values,  $m_i$ , and prey phenotypic values,  $n_j$ , of quantitative traits. Predator traits are normally distributed with mean  $\bar{m}_i = \bar{m}_i(t)$  and constant variances  $\sigma_i^2$ , and prey traits are normally distributed with mean  $\bar{n}_j = \bar{n}_j(t)$  and constant variances  $\beta_j^2$ , i.e., their distributions are given by

$$p(m_i, \bar{m}_i) = \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp \left[ -\frac{(m_i - \bar{m}_i)^2}{2\sigma_i^2} \right] \quad [1]$$

$$p(n_j, \bar{n}_j) = \frac{1}{\sqrt{2\pi\beta_j^2}} \exp \left[ -\frac{(n_j - \bar{n}_j)^2}{2\beta_j^2} \right] \quad [2]$$

These variances have genetic and environmental components:

$$\sigma_i^2 = \sigma_{Gi}^2 + \sigma_{Ei}^2 \quad [3]$$

$$\beta_j^2 = \beta_{Gj}^2 + \beta_{Ej}^2 \quad [4]$$

Assuming predator  $i$  has a linear functional response with attack rate  $a_{ij} = a_{ij}(m_i, n_j)$ , 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

$$\begin{aligned} W_i(N_1, \dots, N_u, M_i, n_1, \dots, n_u, m_i) \\ = \sum_{j=1}^u [e_{ij}(m_i, n_j) a_{ij}(m_i, n_j) N_j] - d_i(m_i) \end{aligned} \quad [5]$$

and the mean fitness of the predator population is

$$\begin{aligned} \bar{W}_i(N_1, \dots, N_u, M_i, \bar{n}_1, \dots, \bar{n}_u, \bar{m}_i) \\ = \int_{\mathbb{R}^{u+1}} W_i p(m_i, \bar{m}_i) \prod_{j=1}^u p(n_j, \bar{n}_j) dm_i \prod_{j=1}^u dn_j \end{aligned} \quad [6]$$

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

$$\begin{aligned} Y_j(N_j, M_1, \dots, M_v, n_j, m_1, \dots, m_v) \\ = r_j(n_j) \left( 1 - \frac{N_j}{K_j(n_j)} \right) - \sum_{i=1}^v [a_{ij}(m_i, n_j) M_i] \end{aligned} \quad [7]$$

and the mean fitness of the prey population is

$$\begin{aligned} \bar{Y}_j(N_j, M_1, \dots, M_v, \bar{n}_j, \bar{m}_1, \dots, \bar{m}_v) \\ = \int_{\mathbb{R}^{v+1}} Y_j p(n_j, \bar{n}_j) \prod_{i=1}^v p(m_i, \bar{m}_i) dn_j \prod_{i=1}^v dm_i \end{aligned} \quad [8]$$

Thus the complete ditrophic model of  $v$  predator species and  $u$  prey species is given by

$$\frac{dM_i}{dt} = M_i \bar{W}_i \quad [9a]$$

$$\frac{dN_j}{dt} = N_j \bar{Y}_j \quad [9b]$$

$$\frac{d\bar{m}_i}{dt} = \sigma_{Gi}^2 \frac{\partial \bar{W}_i}{\partial \bar{m}_i} \quad [9c]$$

$$\frac{d\bar{n}_j}{dt} = \beta_{Gj}^2 \frac{\partial \bar{Y}_j}{\partial \bar{n}_j} \quad [9d]$$

Lande derived [9c] and [9d] under the assumption that the distribution of phenotypes remains Gaussian. [9] is a special case of Kindrik and Kondrashov's general model of coevolution [3]. The defining feature of our model is the distinction between trophic levels, of which we are assuming there are two. In the following sections we derive two manifestations of [9] by explicitly defining the parameter functions.

## Model 1

This first example is a coevolutionary analog of Schreiber, Bürger, and Bolnick's apparent competition model [1]. Assume the prey growth rates and carrying capacities,  $r_j$  and

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$K_j$ , 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.,

$$a_{ij}(m_i, n_j) = \alpha_{ij} \exp \left[ -\frac{((m_i - n_j) - \theta_{ij})^2}{2\tau_{ij}^2} \right] \quad [10]$$

where  $\alpha_{ij}$  is the maximal attack and  $\tau_{ij}$  determines how steeply the attack rate declines with distance from the optimal trait difference  $\theta_{ij}$ . In effect,  $\tau_{ij}$  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

$$\begin{aligned} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) &= \int_{\mathbb{R}^2} a_{ij}(m_i, n_j) p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i dn_j \\ &= \frac{\alpha_{ij} \tau_{ij}}{\sqrt{A_{ij}}} \exp \left[ -\frac{((\overline{m_i} - \overline{n_j}) - \theta_{ij})^2}{2A_{ij}} \right] \end{aligned} \quad [11]$$

where  $A_{ij} = \tau_{ij}^2 + \sigma_i^2 + \beta_j^2$ . [6] and [8] yield explicit formulas for  $\overline{W_i}$  and  $\overline{Y_j}$ :

$$\overline{W_i} = \sum_{j=1}^u [e_{ij} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) N_j] - d_i \quad [12]$$

$$\overline{Y_j} = r_j \left( 1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^v [\overline{a_{ij}}(\overline{m_i}, \overline{n_j}) M_i] \quad [13]$$

The right-hand sides of [9c] and [9d] can also be found:

$$\frac{\partial \overline{W_i}}{\partial \overline{m_i}} = \sum_{j=1}^u \left[ \frac{e_{ij} N_j (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \quad [14]$$

$$\frac{\partial \overline{Y_j}}{\partial \overline{n_j}} = \sum_{i=1}^v \left[ \frac{M_i (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \quad [15]$$

Thus [9] simplifies:

$$\frac{dM_i}{dt} = M_i \left[ \sum_{j=1}^u [e_{ij} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) N_j] - d_i \right] \quad [16a]$$

$$\frac{dN_j}{dt} = N_j \left[ r_j \left( 1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^v [\overline{a_{ij}}(\overline{m_i}, \overline{n_j}) M_i] \right] \quad [16b]$$

$$\frac{d\overline{m_i}}{dt} = \sigma_{Gi}^2 \sum_{j=1}^u \left[ \frac{e_{ij} N_j (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \quad [16c]$$

$$\frac{d\overline{n_j}}{dt} = \beta_{Gj}^2 \sum_{i=1}^v \left[ \frac{M_i (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \quad [16d]$$

If there is only one predator species and one prey species, then [16] simplifies:

$$\frac{dM}{dt} = M [e\overline{a}(\overline{m}, \overline{n})N - d] \quad [17a]$$

$$\frac{dN}{dt} = N \left[ r \left( 1 - \frac{N}{K} \right) - \overline{a}(\overline{m}, \overline{n})M \right] \quad [17b]$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{eN(\theta - (\overline{m} - \overline{n}))}{A} \overline{a}(\overline{m}, \overline{n}) \quad [17c]$$

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{M(\theta - (\overline{m} - \overline{n}))}{A} \overline{a}(\overline{m}, \overline{n}) \quad [17d]$$

## 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.

$$r_j(n_j) = \rho_j \exp \left[ -\frac{(n_j - \phi_j)^2}{2\gamma_j^2} \right] \quad [18]$$

where  $\rho$  is the maximal growth rate and  $\gamma_j$  determines how steeply the growth rate declines with distance from the optimal trait value  $\phi_j$ . In effect,  $\gamma_j$  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

$$\begin{aligned} \overline{r_j}(\overline{n_j}) &= \int_{\mathbb{R}} r_j(n_j) p(n_j, \overline{n_j}) dn_j \\ &= \frac{\rho_j \gamma_j}{\sqrt{B_j}} \exp \left[ -\frac{(\overline{n_j} - \phi_j)^2}{2B_j} \right] \end{aligned} \quad [19]$$

where  $B_j = \beta_j^2 + \gamma_j^2$ . Since  $\overline{W_i}$  is not dependent on  $r_j$ , [12] suffices, but since  $\overline{Y_j}$  is dependent on  $r_j$ , it must be recalculated. [8] yields

$$\overline{Y_j} = \overline{r_j}(\overline{n_j}) \left( 1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^v [\overline{a_{ij}}(\overline{m_i}, \overline{n_j}) M_i] \quad [20]$$

Since  $\overline{W_i}$  did not change from Model 1, [16c] is sufficient for the right hand side of [9c]. However, the right hand side of [9d] must be recalculated.

$$\begin{aligned} \frac{\partial \overline{Y_j}}{\partial \overline{n_j}} &= \overline{r_j}(\overline{n_j}) \left( 1 - \frac{N_j}{K_j} \right) \frac{\phi_j - \overline{n_j}}{B_j} \\ &+ \sum_{i=1}^v \left[ \frac{M_i (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \end{aligned} \quad [21]$$

Thus [9] simplifies:

$$\frac{dM_i}{dt} = M_i \left[ \sum_{j=1}^u [e_{ij} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) N_j] - d_i \right] \quad [22a]$$

$$\frac{dN_j}{dt} = N_j \left[ \overline{r_j}(\overline{n_j}) \left( 1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^v [\overline{a_{ij}}(\overline{m_i}, \overline{n_j}) M_i] \right] \quad [22b]$$

$$\frac{d\overline{m_i}}{dt} = \sigma_{Gi}^2 \sum_{j=1}^u \left[ \frac{e_{ij} N_j (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \quad [22c]$$

$$\begin{aligned} \frac{d\overline{n_j}}{dt} &= \beta_{Gj}^2 \left[ \overline{r_j}(\overline{n_j}) \left( 1 - \frac{N_j}{K_j} \right) \frac{\phi_j - \overline{n_j}}{B_j} \right. \\ &+ \left. \sum_{i=1}^v \left[ \frac{M_i (\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{A_{ij}} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \right] \end{aligned} \quad [22d]$$

If there is only one predator species and one prey species, then [22] simplifies:

$$\frac{dM}{dt} = M [e\bar{a}(\bar{m}, \bar{n})N - d] \quad [23a]$$

$$\frac{dN}{dt} = N \left[ \bar{r}(\bar{n}) \left( 1 - \frac{N}{K} \right) - \bar{a}(\bar{m}, \bar{n})M \right] \quad [23b]$$

$$\frac{d\bar{m}_i}{dt} = \sigma_G^2 \frac{eN(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \quad [23c]$$

$$\begin{aligned} \frac{d\bar{n}}{dt} = \beta_G^2 \left[ \bar{r}(\bar{n}) \left( 1 - \frac{N}{K} \right) \frac{\phi - \bar{n}}{B} \right. \\ \left. + \frac{M(\theta - (\bar{m} - \bar{n}))}{A} \bar{a}(\bar{m}, \bar{n}) \right] \quad [23d] \end{aligned}$$

## Results

### Model 1.

#### Pairwise Predator-Prey Dynamics

There are three classifications of equilibrium of [17]: extinction, exclusion, and coexistence. There are an infinite amount of equilibrium points for each of these three classifications. Extinction equilibria are given by

$$(M^*, N^*, \bar{m}^*, \bar{n}^*) = (0, 0, \mu^*, \nu^*) \quad [24]$$

where  $\mu^*$  and  $\nu^*$  are arbitrary values. Exclusion equilibria are given by

$$(M^*, N^*, \bar{m}^*, \bar{n}^*) = (0, K, \mu^* + \theta, \mu^*) \quad [25]$$

where  $\mu^*$  is an arbitrary value. Coexistence equilibria are given by

$$\begin{aligned} (M^*, N^*, \bar{m}^*, \bar{n}^*) = \\ \left( \frac{r\sqrt{A}}{\alpha\tau} \left( 1 - \frac{N^*}{K} \right), \frac{d\sqrt{A}}{e\alpha\tau}, \mu^* + \theta, \mu^* \right) \quad [26] \end{aligned}$$

where  $\mu^*$  is an arbitrary value. Local stability analysis yields that all extinction equilibria are unstable, exclusion equilibria are asymptotically stable if

$$d > \frac{Ke\alpha\tau}{\sqrt{A}} \quad [27]$$

and coexistence equilibria are asymptotically stable if

$$\frac{\sigma_G^2}{\beta_G^2} > \frac{r}{d} \left( 1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right) \quad [28]$$

Intuitively, exclusion is stable if the predator death rate is high enough. Note that if [27] holds then [26] is not biologically feasible ( $M^* < 0$ ), and so even though [28] would hold, it would be irrelevant. Since  $\sigma_G^2/\beta_G^2$  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 [27] and [28] are not equal and opposite conditions, there is at least one type of non-equilibrium coexistence dynamic. Numerical simulations provide insight into these dynamics (Figure 3). This simulation 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.

### Model 2.

#### Pairwise Predator-Prey Dynamics

Similarly to [17], there are three classifications of equilibrium of system [23]: extinction, exclusion, and coexistence. There are an infinite amount of equilibrium points for the extinction and exclusion classifications, but stabilizing selection provides a unique equilibrium point for coexistence. Extinction equilibria are given by [24], and exclusion equilibria are given by [25]. The coexistence equilibrium is given by

$$\begin{aligned} (M^*, N^*, \bar{m}^*, \bar{n}^*) = \\ \left( \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}} \left( 1 - \frac{N^*}{K} \right), \frac{d\sqrt{A}}{e\alpha\tau}, \phi + \theta, \phi \right) \quad [29] \end{aligned}$$

Local stability analysis yields that all extinction equilibria are unstable, exclusion equilibria are asymptotically stable if [27] holds, and the coexistence equilibrium is asymptotically stable if

$$\frac{\sigma_G^2}{\beta_G^2} > \frac{\rho\gamma}{d\sqrt{B}} \left( 1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right) \left( 1 - \frac{A}{B} \right) \quad [30]$$

Intuitively, exclusion is stable if the predator death rate is high enough. Similar to Model 1, if [27] holds then [29] is not biologically feasible ( $M^* < 0$ ), and so even though [30] may hold, it would be irrelevant. Again, since  $\sigma_G^2/\beta_G^2$  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.

[27] and [30] 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).

## Appendix

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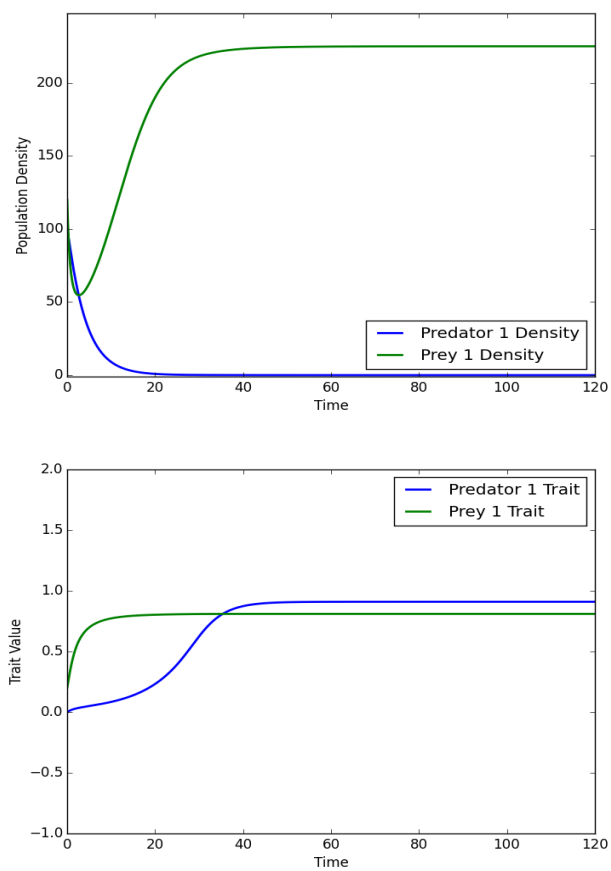
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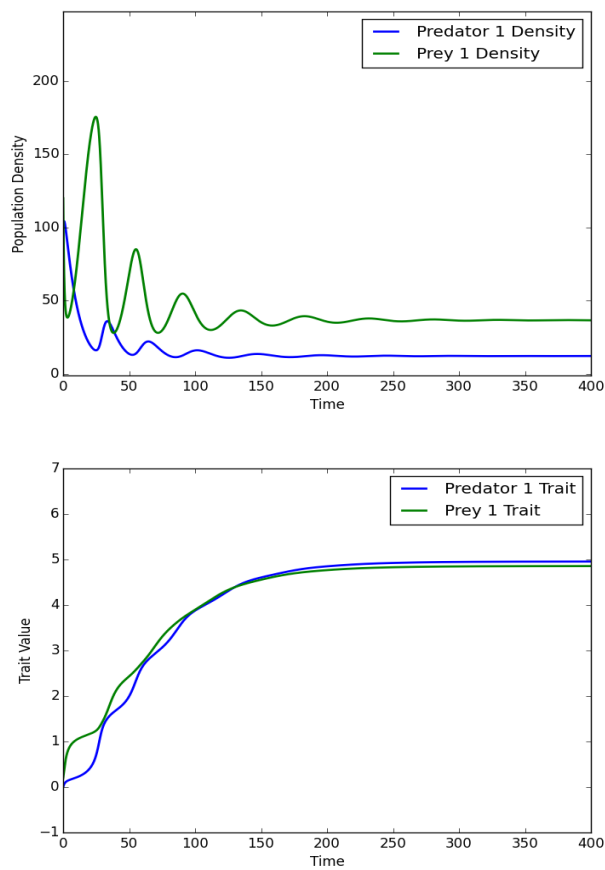
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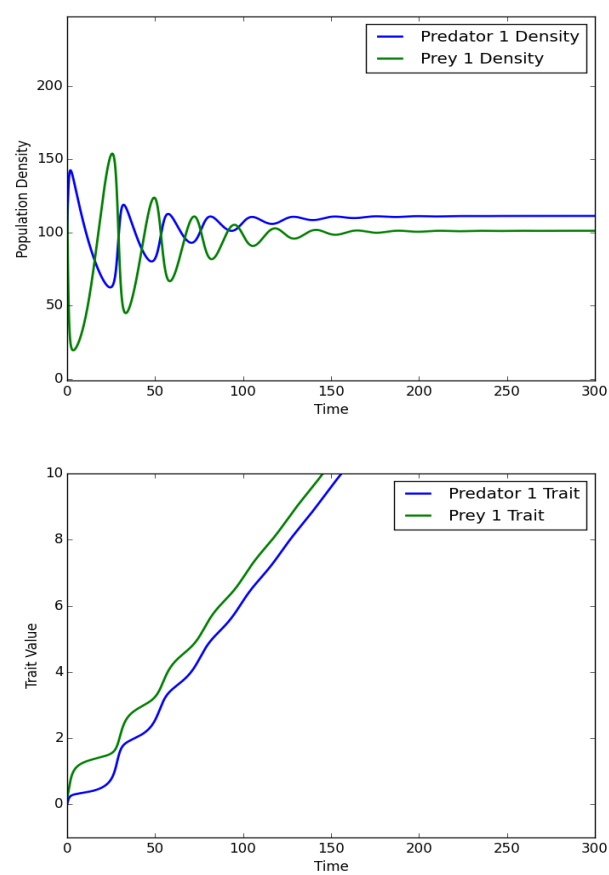
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**Fig. 1.** Model 1: Exclusion Equilibrium



**Fig. 2.** Model 1: Coexistence Equilibrium



**Fig. 3.** Model 1: Non-Equilibrium Coexistence

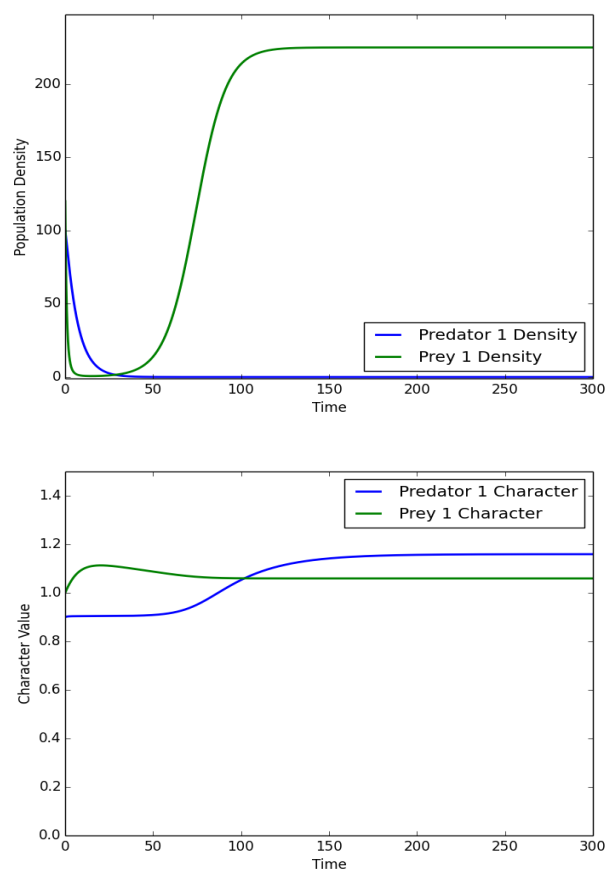
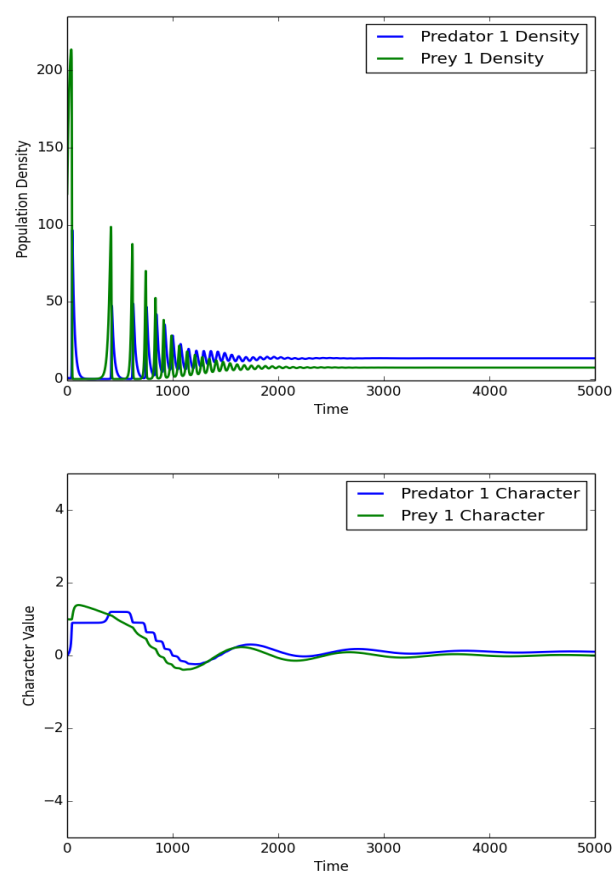
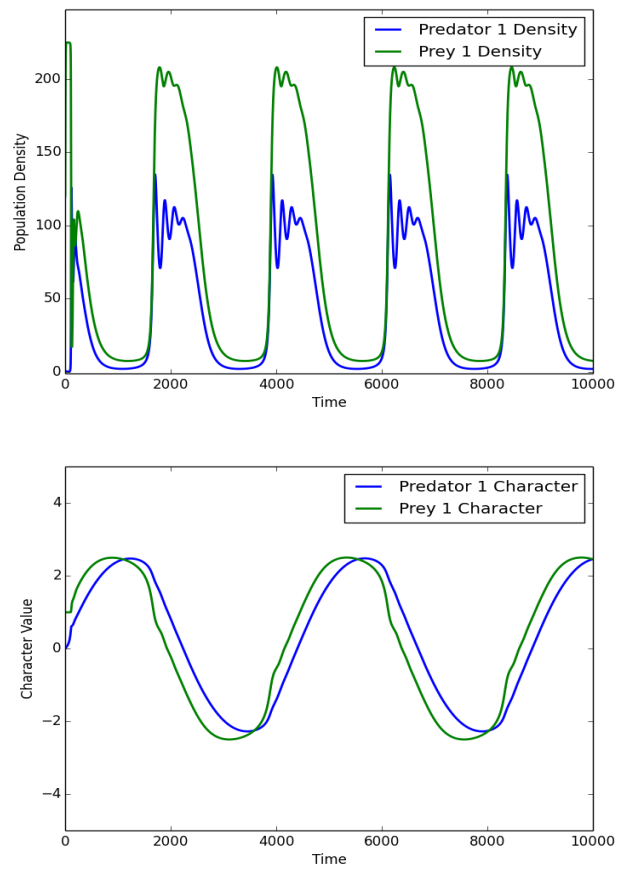


Fig. 4. Model 2: Exclusion Equilibrium





**Fig. 5.** Model 2: Coexistence Equilibrium



**Fig. 6.** Model 2: Non-Equilibrium, Cyclic Coexistence