

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 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

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

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

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, 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.

Model 1

This first model is a coevolutionary analog of Schreiber, Bürger, and Bolnick's model. We assume r_j , K_j , d_i , and e_{ij} are constant, but an individual predator's attack rate on an individual prey $a_{ij}(m_i, n_j)$ is maximal at an optimal trait difference, $m_i - n_j = \theta_{ij}$, and decreases away from this optimal trait difference in a Gaussian manner, i.e.,

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

Reserved for Publication Footnotes

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

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

where $A_{ij} = \tau_{ij}^2 + \sigma_i^2 + \beta_j^2$. Explicit formulas for $\overline{W_i}$ and $\overline{Y_j}$ can be found:

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

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

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] is simplified to:

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

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

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

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

If there is only one predator species and one prey species, then [16] is simplified to

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

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

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

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

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 ρ is the maximal growth rate 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 dependent prey j is on its optimal trait value. 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 $\overline{W_i}$ does not include r_j , it still given by [12], but $\overline{Y_j}$ must be recalculated.

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

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.

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

Thus [9] is simplified to:

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

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

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

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

If there is only one predator species and one prey species, then [22] is simplified to

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

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

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

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

Results

Model 1.

Pairwise Predator-Prey Dynamics

There are three classifications of equilibrium of system [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 μ^* and ν^* are arbitrary values. Exclusion equilibria are given by

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

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

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

where μ^* 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 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 displays a simulation that results in stable exclusion, and figure 6 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. We currently cannot analytically determine exactly what this dynamic is, but numerical simulations provide intuition - see figure 7.

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 a single equilibrium point for the coexistence equilibrium. Extinction equilibria are given by [24], and exclusion equilibria are given by [25]. The coexistence equilibrium is given by

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

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. Note that if [27] holds then [29] is not biologically feasible ($M^* < 0$), and so even though [30] may hold, 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 displays a simulation that results in stable exclusion, and figure 6 displays a simulation that results in stable coexistence.

Since [27] and [30] are not equal and opposite conditions, there is at least one type of non-equilibrium coexistence dynamic. We currently cannot analytically determine exactly what this dynamic is, but numerical simulations provide intuition - see figure 7.

Simulations.

Simulation 1

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Simulation 2

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Discussion

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Materials and Methods

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Definition 1. A bounded function θ is a weak solution of QG if for any $\phi \in C_0^\infty(\mathbb{R}/\mathbb{Z} \times \mathbb{R} \times [0, \varepsilon])$ we have

$$\int_{\mathbb{R}^+ \times \mathbb{R}/\mathbb{Z} \times \mathbb{R}} \theta(x, y, t) \partial_t \phi(x, y, t) dy dx dt + \int_{\mathbb{R}^+ \times \mathbb{R}/\mathbb{Z} \times \mathbb{R}} \theta(x, y, t) u(x, y, t) \cdot \nabla \phi(x, y, t) dy dx dt = 0 \quad [31]$$

where u is determined previously.

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Theorem 1. If the active scalar θ satisfies the equation [31], then φ satisfies the equation

$$\begin{aligned} \frac{\partial \varphi}{\partial t}(x, t) &= \int_{\mathbb{R}/\mathbb{Z}} \frac{\frac{\partial \varphi}{\partial x}(x, t) - \frac{\partial \varphi}{\partial u}(u, t)}{[(x - u)^2 + (\varphi(x, t) - \varphi(u, t))^2]^{\frac{1}{2}}} \\ &\quad \chi(x - u, \varphi(x, t) - \varphi(u, t)) du + \\ &\quad + \int_{\mathbb{R}/\mathbb{Z}} \left[\frac{\partial \varphi}{\partial x}(x, t) - \frac{\partial \varphi}{\partial u}(u, t) \right] \\ &\quad \eta(x - u, \varphi(x, t) - \varphi(u, t)) du + \text{Error} \quad [32] \end{aligned}$$

with $|\text{Error}| \leq C \delta |\log \delta|$ where C depends only on $\|\theta\|_{L^\infty}$ and $\|\nabla \varphi\|_{L^\infty}$.

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Appendix

An appendix without a title.

Appendix: Appendix title

An appendix with a title.

ACKNOWLEDGMENTS. This work was partially supported by a grant from the Spanish Ministry of Science and Technology.

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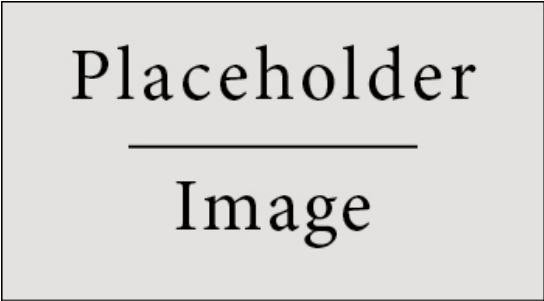


Fig. 1. Figure caption

Table 1. Table caption

| Treatments | Response 1 | Response 2 |
|-------------|------------|------------|
| Treatment 1 | 0.0003262 | 0.562 |
| Treatment 2 | 0.0015681 | 0.910 |
| Treatment 3 | 0.0009271 | 0.296 |

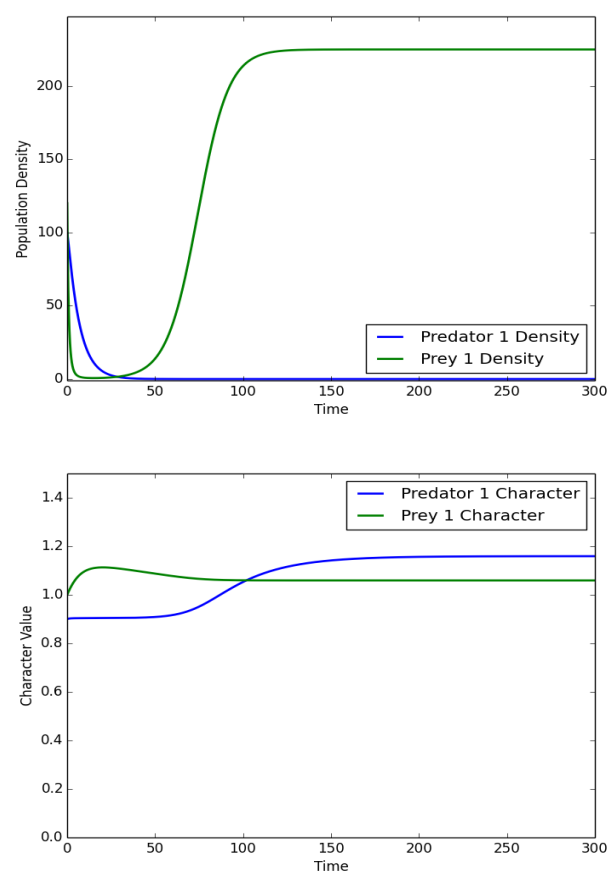


Fig. 2. Model 2: Exclusion Equilibrium

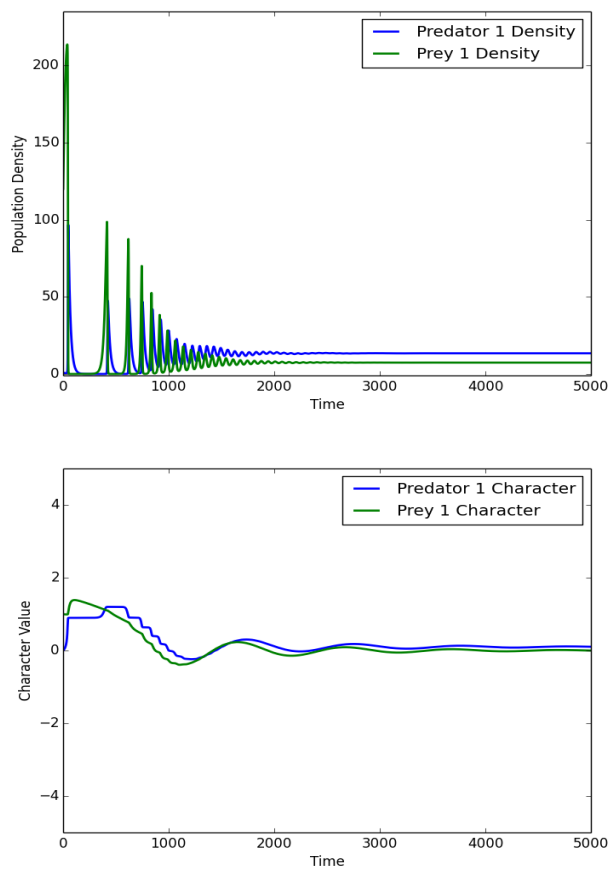


Fig. 3. Model 2: Coexistence Equilibrium

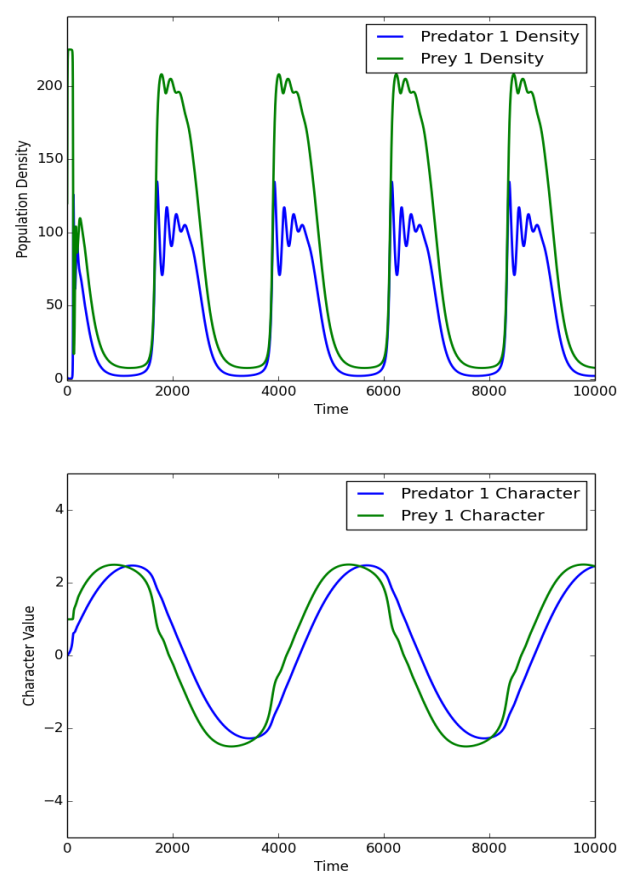


Fig. 4. Model 2: Non-Equilibrium, Cyclic Coexistence

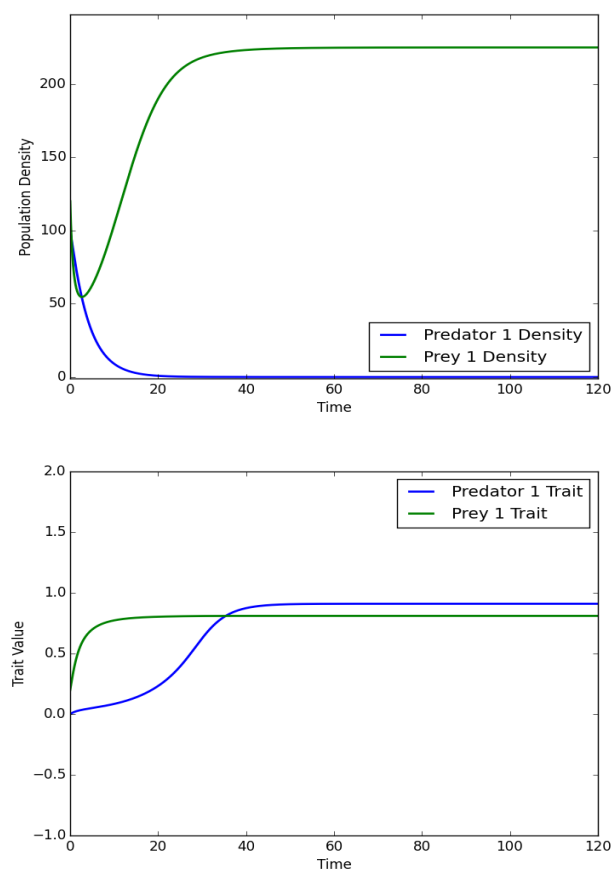


Fig. 5. Model 1: Exclusion Equilibrium

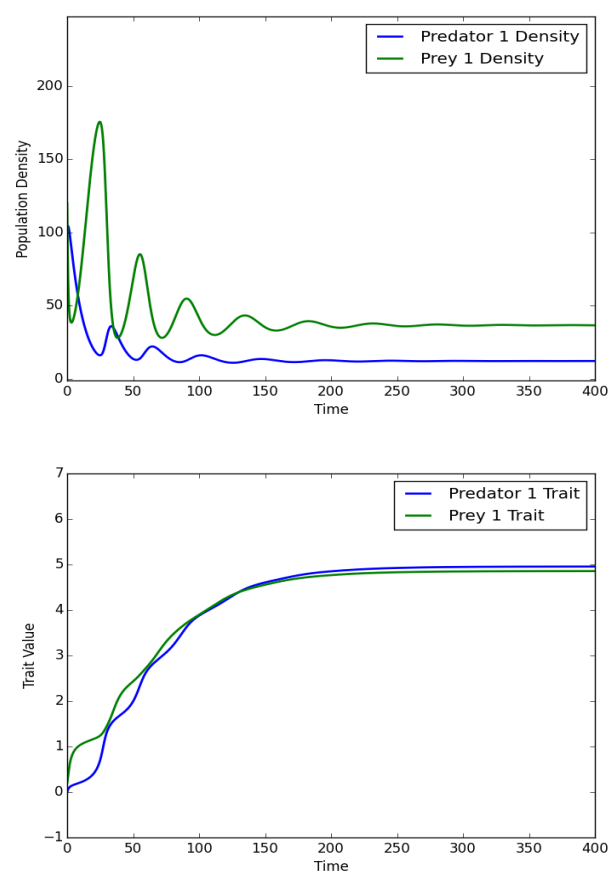


Fig. 6. Model 1: Coexistence Equilibrium

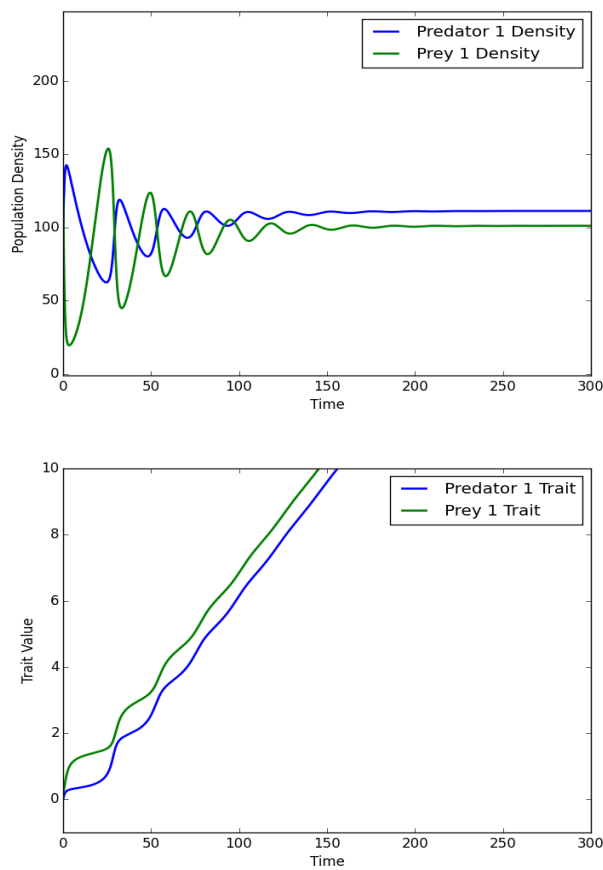


Fig. 7. Model 1: Non-Equilibrium Coexistence