

Example: The Lotka - Volterra cannibalism time budget model

Resident dynamics:

$$\frac{d}{dt} R = r R \left(1 - \frac{R}{K}\right) - \alpha R \sum_{j=1}^l (1 - x_j) n_j$$

$$\frac{d}{dt} n_i = \epsilon \alpha R (1 - x_i) n_i - \delta n_i +$$

$$\gamma \beta[x_i] x_i n_i \sum_{j=1}^l (1 - x_j) n_j - (1 - x_i) n_i \sum_{j=1}^l \beta[x_j] x_j n_j$$

$$(i = 1, \dots, l)$$

MONOMORPHIC RESIDENT POPULATION

Monomorphic resident population dynamics:
(R = resource density; n = resident population density)

$$d\text{Log}R = r - r R / k - \alpha (1 - x) n;$$

$$d\text{Log}n = \epsilon \alpha (1 - x) R - \delta + \gamma \beta[x] x (1 - x) n - (1 - x) \beta[x] x n;$$

Monomorphic resident population equilibrium:

$$\text{Solve}[\{0 = r - r R / k - \alpha (1 - x) n, \\ 0 = \epsilon \alpha (1 - x) R - \delta + \gamma \beta[x] x (1 - x) n - (1 - x) \beta[x] x n\}, \\ \{R, n\}]$$

$$\left\{ \left\{ R \rightarrow -\frac{k \alpha \delta + k r x \beta[x] - k r x \gamma \beta[x]}{-k \alpha^2 \epsilon + k x \alpha^2 \epsilon - r x \beta[x] + r x \gamma \beta[x]}, \right. \right.$$

$$\left. n \rightarrow -\frac{r \delta - k r \alpha \epsilon + k r x \alpha \epsilon}{(-1 + x) (-k \alpha^2 \epsilon + k x \alpha^2 \epsilon - r x \beta[x] + r x \gamma \beta[x])} \right\}$$

$$R[x_] := -\frac{k (\alpha \delta - r x (-1 + \gamma) \beta[x])}{k (-1 + x) \alpha^2 \epsilon + r x (-1 + \gamma) \beta[x]};$$

$$n[x_] := -\frac{r (\delta + k (-1 + x) \alpha \epsilon)}{(-1 + x) (k (-1 + x) \alpha^2 \epsilon + r x (-1 + \gamma) \beta[x])};$$

Invasion fitness and its derivatives:

$$s_{\text{mo}}[x_ , y_] := \epsilon \alpha (1 - y) R[x] - \delta + \gamma \beta[y] y (1 - x) n[x] -$$

$$(1 - y) \beta[x] x n[x];$$

$$ds_{\text{mo}}[x_] := (\partial_y s_{\text{mo}}[x, y]) /. \{y \rightarrow x\};$$

$$dds_{\text{mo}}[x_] := (\partial_y \partial_y s_{\text{mo}}[x, y]) /. \{y \rightarrow x\};$$

Parameter values and functions:

$$\alpha = 1; \gamma = 0.2; \delta = 0.1; \epsilon = 0.1; r = 1; k = 10;$$

$$\beta[x_] := 2 - 9 (0.03 + x)^p (1 - x)^q;$$

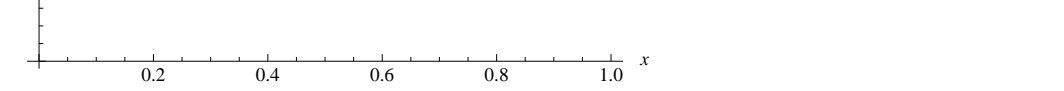
$$p = 1; q = 2.5;$$

$$\text{Plot}[\beta[x], \{x, 0, 1\}, \text{PlotStyle} \rightarrow \{\text{Thick}\}, \\ \text{AxesOrigin} \rightarrow \{0, 0\}, \text{AxesLabel} \rightarrow \{x, \beta\}]$$



Pairwise invadability plot (PIP):

$$\text{ContourPlot}[\{n[x], \text{If}[n[x] > 0, s_{\text{mo}}[x, y]]\}, \{x, 0, 1\}, \\ \{y, 0, 1\}, \text{Contours} \rightarrow \{0\}, \\ \text{ContourStyle} \rightarrow \{\{\text{Black}, \text{Thick}, \text{Dashed}\}, \{\text{Black}, \text{Thick}\}\}, \\ \text{PlotPoints} \rightarrow 100]$$



DIMORPHIC RESIDENT POPULATION

Reset:

$$\text{Clear}[\alpha, \beta, \gamma, \delta, \epsilon, r, k];$$

Dimorphic resident population equilibrium:

$$\text{equ} =$$

$$\{0 = r - r R / k - \alpha ((1 - x1) n1 + (1 - x2) n2), \\ 0 = \epsilon \alpha (1 - x1) R - \delta + \gamma \beta[x1] x1 ((1 - x1) n1 + (1 - x2) n2) - \\ (1 - x1) (\beta[x1] x1 n1 + \beta[x2] x2 n2), \\ 0 = \epsilon \alpha (1 - x2) R - \delta + \gamma \beta[x2] x2 ((1 - x1) n1 + (1 - x2) n2) - \\ (1 - x2) (\beta[x1] x1 n1 + \beta[x2] x2 n2)\};$$

$$\text{var} = \{R, n1, n2\};$$

$$\text{Solve}[\text{equ}, \text{var}];$$

$$\text{Simplify}[\%]$$

$$\left\{ \left\{ R \rightarrow \frac{k ((x1 - x2) \alpha \delta + r x1 (-1 + x2) \gamma \beta[x1] - r (-1 + x1) x2 \gamma \beta[x2])}{r \gamma (x1 (-1 + x2) \beta[x1] - (-1 + x1) x2 \beta[x2])}, \right. \right.$$

$$n1 \rightarrow \frac{(k (x1 - x2) (-1 + x2) \alpha^2 \delta \epsilon + r x1 (-1 + x2) \gamma (\delta + k (-1 + x2) \alpha \epsilon) \beta[x1] + \\ r x2 (\gamma (\delta - k \alpha \epsilon) + x2 (\delta - \gamma \delta + k \alpha \gamma \epsilon) - x1 (\delta + k (-1 + x2) \alpha \gamma \epsilon)) \beta[x2]) /}{(r \gamma (x1 (-1 + x2) \beta[x1] - (-1 + x1) x2 \beta[x2])^2)},$$

$$n2 \rightarrow \frac{(r x1 (-x2 \delta + \gamma \delta - k \alpha \gamma \epsilon + k x2 \alpha \gamma \epsilon + x1 (\delta - \gamma \delta - k (-1 + x2) \alpha \gamma \epsilon)) \beta[x1] - \\ (-1 + x1) (k (x1 - x2) \alpha^2 \delta \epsilon - r x2 \gamma (\delta + k (-1 + x1) \alpha \epsilon) \beta[x2])) /}{(r \gamma (x1 (-1 + x2) \beta[x1] - (-1 + x1) x2 \beta[x2])^2)} \};$$

$$R[\{x1_ , x2_ \}] :=$$

$$\frac{(k ((x1 - x2) \alpha \delta + r x1 (-1 + x2) \gamma \beta[x1] - \\ r (-1 + x1) x2 \gamma \beta[x2])) /}{(r \gamma (x1 (-1 + x2) \beta[x1] - (-1 + x1) x2 \beta[x2]))};$$

$$n1[\{x1_ , x2_ \}] :=$$

$$\frac{(k (x1 - x2) (-1 + x2) \alpha^2 \delta \epsilon + \\ r x1 (-1 + x2) \gamma (\delta + k (-1 + x2) \alpha \epsilon) \beta[x1] + \\ r x2 (\gamma (\delta - k \alpha \epsilon) + x2 (\delta - \gamma \delta + k \alpha \gamma \epsilon) - \\ x1 (\delta + k (-1 + x2) \alpha \gamma \epsilon)) \beta[x2]) /}{(r \gamma (x1 (-1 + x2) \beta[x1] - (-1 + x1) x2 \beta[x2])^2)};$$

$$n2[\{x1_ , x2_ \}] :=$$

$$\frac{(r x1 (-x2 \delta + \gamma \delta - k \alpha \gamma \epsilon + k x2 \alpha \gamma \epsilon + \\ x1 (\delta - \gamma \delta - k (-1 + x2) \alpha \gamma \epsilon)) \beta[x1] - \\ (-1 + x1) \\ (k (x1 - x2) \alpha^2 \delta \epsilon - r x2 \gamma (\delta + k (-1 + x1) \alpha \epsilon) \beta[x2])) /}{(r \gamma (x1 (-1 + x2) \beta[x1] - (-1 + x1) x2 \beta[x2])^2)};$$

Dimorphic invasion fitness and derivatives:

$$s_{\text{di}}[\{x1_ , x2_ \}, y_] :=$$

$$\epsilon \alpha (1 - y) R[\{x1, x2\}] - \delta + \\ \gamma \beta[y] y ((1 - x1) n1[\{x1, x2\}] + (1 - x2) n2[\{x1, x2\}]) - \\ (1 - y) (\beta[x1] x1 n1[\{x1, x2\}] + \beta[x2] x2 n2[\{x1, x2\}]);$$

$$x1 ds_{\text{di}}[\{x1_ , x2_ \}] := (\partial_y s_{\text{di}}[\{x1, x2\}, y]) /. \{y \rightarrow x1\};$$

$$x2 ds_{\text{di}}[\{x1_ , x2_ \}] := (\partial_y s_{\text{di}}[\{x1, x2\}, y]) /. \{y \rightarrow x2\};$$

$$x1 dds_{\text{di}}[\{x1_ , x2_ \}] := (\partial_y \partial_y s_{\text{di}}[\{x1, x2\}, y]) /. \{y \rightarrow x1\};$$

$$x2 dds_{\text{di}}[\{x1_ , x2_ \}] := (\partial_y \partial_y s_{\text{di}}[\{x1, x2\}, y]) /. \{y \rightarrow x2\};$$

Default parameter values and functions :

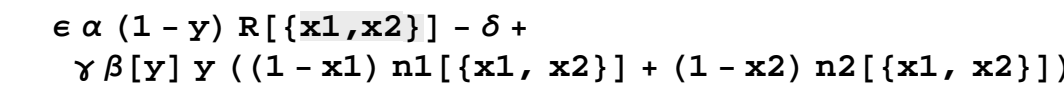
$$\alpha = 1; \gamma = 0.2; \delta = 0.1; \epsilon = 0.1; r = 1; k = 10;$$

$$\beta[x_] := 2 - 9 (0.03 + x)^p (1 - x)^q;$$

$$p = 1; q = 2.5;$$

Coexistence plot:

$$\text{CoexSet} = \text{ContourPlot}[n1[\{x1, x2\}] n2[\{x1, x2\}], \\ \{x1, 0, 1\}, \{x2, 0, 1\}, \text{Contours} \rightarrow \{0\}, \\ \text{ContourStyle} \rightarrow \{\text{Black}, \text{Thick}\}, \text{ContourShading} \rightarrow \text{False}, \\ \text{PlotPoints} \rightarrow 100]$$



Isocline plot:

(solid = x1-isocline; dashed = x2-isocline; black = evolutionarily stable; red = not evolutionarily stable)

$$\text{isoLES} = \text{ContourPlot}[\\ \text{If}[n1[\{x1, x2\}] > 0 \& \& n2[\{x1, x2\}] > 0 \& \& \\ x1 dds_{\text{di}}[\{x1, x2\}] \leq 0, x1 ds_{\text{di}}[\{x1, x2\}]], \\ \{x1, 0, 1\}, \{x2, 0, 1\}, \text{Contours} \rightarrow \{0\}, \\ \text{ContourShading} \rightarrow \text{False}, \text{ContourStyle} \rightarrow \{\text{Black}, \text{Thick}\}, \\ \text{PlotPoints} \rightarrow 30];$$

$$\text{iso1NES} = \\ \text{ContourPlot}[\\ \text{If}[n1[\{x1, x2\}] > 0 \& \& n2[\{x1, x2\}] > 0 \& \& \\ x1 dds_{\text{di}}[\{x1, x2\}] > 0, x1 ds_{\text{di}}[\{x1, x2\}]], \\ \{x1, 0, 1\}, \{x2, 0, 1\}, \text{Contours} \rightarrow \{0\}, \\ \text{ContourShading} \rightarrow \text{False}, \text{ContourStyle} \rightarrow \{\text{Red}, \text{Thick}\}, \\ \text{PlotPoints} \rightarrow 30];$$

$$\text{iso2ES} = \text{ContourPlot}[\\ \text{If}[n1[\{x1, x2\}] > 0 \& \& n2[\{x1, x2\}] > 0 \& \& \\ x2 dds_{\text{di}}[\{x1, x2\}] \leq 0, x2 ds_{\text{di}}[\{x1, x2\}]], \\ \{x1, 0, 1\}, \{x2, 0, 1\}, \text{Contours} \rightarrow \{0\}, \\ \text{ContourShading} \rightarrow \text{False}, \\ \text{ContourStyle} \rightarrow \{\text{Black}, \text{Thick}, \text{Dashed}\}, \\ \text{PlotPoints} \rightarrow 30];$$

$$\text{iso2NES} = \\ \text{ContourPlot}[\\ \text{If}[n1[\{x1, x2\}] > 0 \& \& n2[\{x1, x2\}] > 0 \& \& \\ x2 dds_{\text{di}}[\{x1, x2\}] > 0, x2 ds_{\text{di}}[\{x1, x2\}]], \\ \{x1, 0, 1\}, \{x2, 0, 1\}, \text{Contours} \rightarrow \{0\}, \\ \text{ContourShading} \rightarrow \text{False}, \\ \text{ContourStyle} \rightarrow \{\text{Red}, \text{Thick}, \text{Dashed}\}, \text{PlotPoints} \rightarrow 30];$$

$$\text{Show}[\text{CoexSet}, \text{isoLES}, \text{iso1NES}, \text{iso2ES}, \text{iso2NES}]$$

