Ecological Dynamics

Predation (1 / 2)

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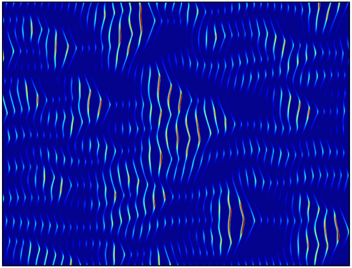
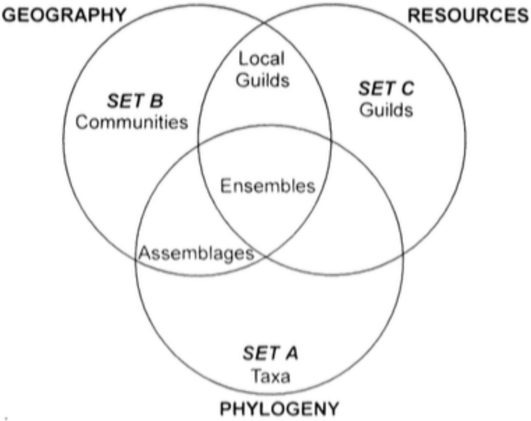
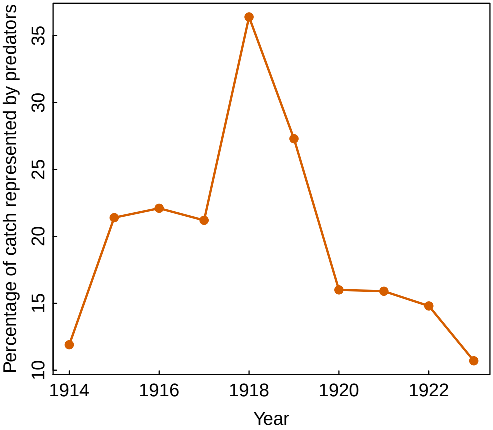


Defining trophic communities (Fauth et al., 1996)



Predation is a process that typically involves species belonging to different guilds (i.e., species occupying different trophic levels).

A motivating example: fish abundance in the Adriatic



Umberto D'Ancona observed the above trends in the frequency of predators in the Adriatic Sea during World War I and asked his father in law Vito Volterra what could cause such fluctuations.

The Lotka-Volterra predator-prey model

Volterra (1931) developed a mathematical model to understand the dynamics of trophically-coupled species:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha N - \beta NP$$
$$\frac{\mathrm{d}P}{\mathrm{d}t} = \delta NP - \gamma P$$

Where α represents the growth rate of the prey N, β the attack rate of the predator P, δ the conversion rate from prey to predator, and γ the mortality rate of the predator.

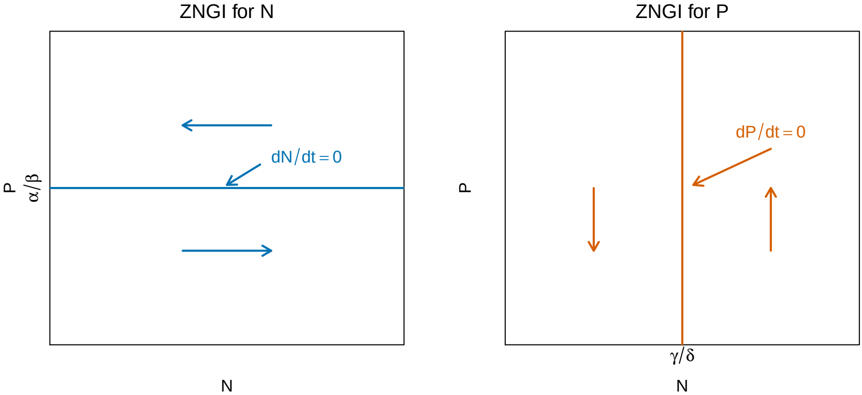
Graphical analysis of the model

The ZNGI can be obtained by setting each differential equation to zero and solving the equilibrium abundance $\hat{N}$ and $\hat{P}$:

$$\hat{N} = \frac{\gamma}{\delta}$$
$$\hat{P} = \frac{\alpha}{\beta}$$

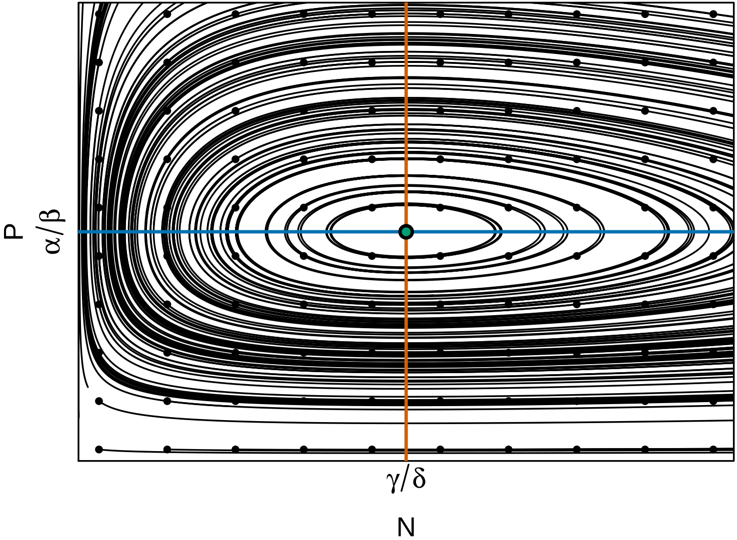
These ZNGI are orthogonal to each other which means that the equilibrium of the prey is determined by the predator and vice versa.

Graphical analysis of the model

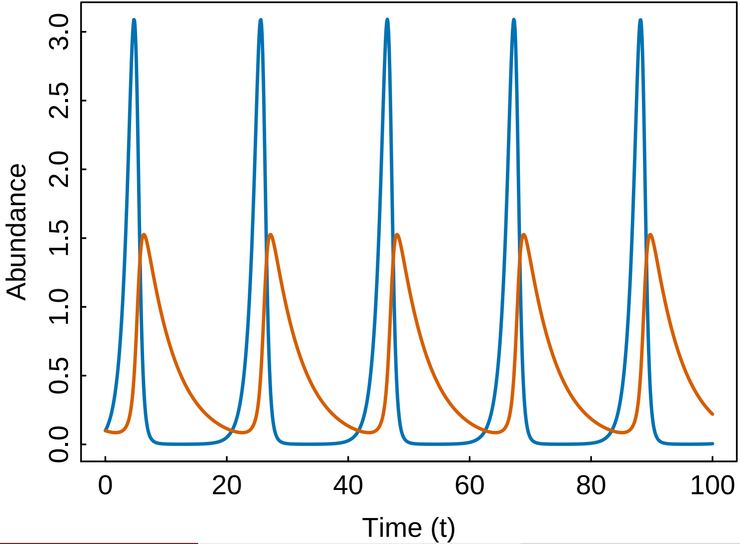


The configuration of these ZNGI leads to neutrally stable oscillations whose center has coordinates $\left\{\hat{N} = \frac{\gamma}{\delta}, \hat{P} = \frac{\alpha}{\beta}\right\}$ and whose amplitude depends on the initial conditions.

Neutrally stable oscillations



Example of predator-prey oscillations



Stability analysis of the model

To assess the stability of the equilibria, we must first write the Jacobian matrix $\mathbf{J}$ by taking the partial derivatives of each population growth rate $\dot{N}$ and $\dot{P}$ with respect to each variable N and P:

$$\mathbf{J} = \begin{bmatrix} \alpha - \beta\hat{P} & -\beta\hat{N} \\ \delta\hat{P} & \delta\hat{N} - \gamma \end{bmatrix}$$

We now assess the stability of the extinction equilibrium $\left\{\hat{N} = 0, \hat{P} = 0\right\}$:

$$\mathbf{J}\,(0,0) = \begin{bmatrix} \alpha & -\beta \\ 0 & -\gamma \end{bmatrix}$$

Stability analysis of the model

To determine the eigenvalues, we subtract $\lambda\mathbf{I}$ from $\mathbf{J}(0,0)$ and find the characteristic polynomial by computing the determinant:

$$0 = (\alpha - \lambda_1)(-\gamma - \lambda_2)$$

There are two solutions to this equation: $\lambda_1 = \alpha$ and $\lambda_2 = -\gamma$. This means that the extinction equilibrium is a saddle point because it will be stable for P as long as $\gamma > 0$ but unstable for N as long as $\alpha > 0$.

Although it is not an equilibrium *per se*, the prey N will grow exponentially in the absence of the predator.

We now determine the stability of the interior equilibrium $\left\{\hat{N} = \frac{\gamma}{\delta}, \hat{P} = \frac{\alpha}{\beta}\right\}$:

$$\mathbf{J}\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right) = \begin{bmatrix} 0 - \lambda & -\beta\frac{\gamma}{\delta} \\ \delta\frac{\alpha}{\beta} & -\lambda \end{bmatrix}$$

Stability analysis of the model

The eigenvalues of $\mathbf{J}\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$ are:

$$0 = \lambda^2 + \alpha\delta$$

We solve for λ by using the quadratic formula with $a = 1$, $b = 0$ and $c = \alpha\gamma$:

$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} = \frac{0 \pm \sqrt{-4\alpha\gamma}}{2}$$

Since $\alpha > 0$ and $\gamma > 0$, the term under the square root is negative, which means that the eigenvalues are complex.

Using $i = \sqrt{-1}$, we can rewrite the eigenvalues as:

$$\boxed{\lambda = 0 \pm i\sqrt{\alpha\gamma}}$$

Stability analysis of the model

Recall that the real part of the eigenvalues controls the exponential rate at which perturbations from the equilibrium grow nor decay over time and the imginary part controls the frequency of the oscillations.

Since the real part of the eigenvalues is zero, the interior equilibrium is neutrally stable, which means that perturbations neither grow nor decay.

Furthermore, the imaginary part of the eigenvalues shows that the system will experience oscillations whose frequency will be controlled by the growth rate of N and the mortality of P.

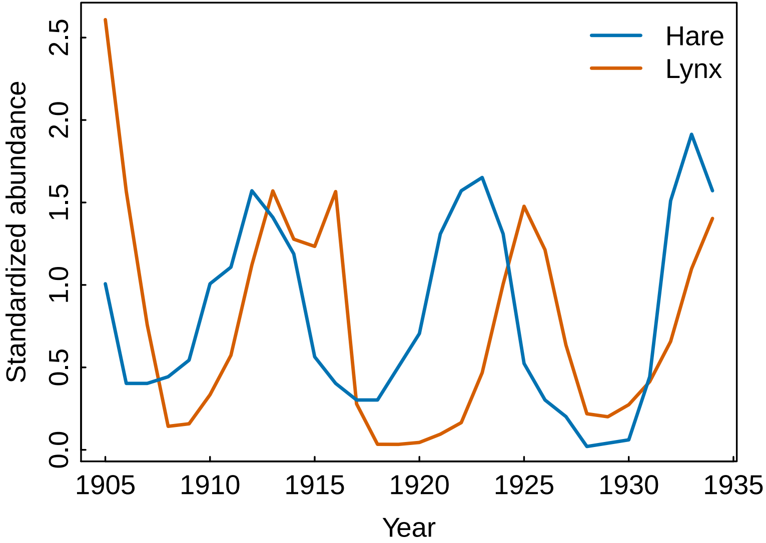
Increasing (decreasing) either α or γ will increase (decrease) the frequency of the oscillations. The period of the oscillations is $\frac{2\pi}{\sqrt{\alpha\gamma}}$.

The Lotka-Volterra model is thus **structurally unstable** in that its interior equilibrium is never a stable point regardless of the parameter values.

Interpreting the results ecologically

- The structural instability of the model makes intuitive sense given its mathematical formulation
- The prey will grow exponentially in the absence of the predator and the predator will growth exponentially if the prey is abundant
- Neither species limits itself via **negative intraspecific feedbacks**, but each species limits the other via **negative interspecific feedbacks** (i.e., orthogonal ZNGI)
- The interplay between the lack of negative intraspecific feedbacks and the strong negative interspecific feedbacks leads to oscillations
- The amplitude of the oscillations will depend on the initial conditions (distance from equilibrium center) and the frequency will depend on the growth rate of the prey and the mortality of the predator

Example of limit cycles: Canadian hare and lynx



Assumptions of Lotka-Volterra model

- **Exponential growth**: the prey species will growth exponentially in the absence of the predator
- **Specialist predator**: the predator is a specialist that can only perist in the presence of the prey
- **Insatiable predator**: individual predators can consume an infinite number of prey
- **Constant parameters**: the model parameters do not vary over time due to demographic or environmental stochasticity
- **Random interactions**: individual predator encounter prey randomly in a homogeneous environment

Adding realism to the model

We can make the model slighly more realistic by adding intraspecific competition for the prey in the form of carrying capacity K:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) - \beta NP$$
$$\frac{\mathrm{d}P}{\mathrm{d}t} = \delta NP - \gamma P$$

This more realistic model has two boundary equilibria and one interior equilibrium. We will now determine their stability.

Analyzing the more realistic model

To assess the stability of the equilibria, we must first write the Jacobian matrix $\mathbf{J}$ by taking the partial derivatives of each population growth rate $\dot{N}$ and $\dot{P}$ with respect to each variable N and P:

$$\mathbf{J} = \begin{bmatrix} \frac{rK-2rN-\beta KP}{K} & -\beta N \\ \delta P & \delta N - \gamma \end{bmatrix}$$

We now assess the stability of the extinction equilibrium $\left\{\hat{N} = 0, \hat{P} = 0\right\}$:

$$\mathbf{J}\,(0,0) = \begin{bmatrix} r & 0 \\ 0 & -\gamma \end{bmatrix}$$

Analyzing the more realistic model

To determine the eigenvalues, we subtract $\lambda\mathbf{I}$ from $\mathbf{J}(0,0)$ and find the characteristic polynomial by computing the determinant:

$$0 = (r - \lambda_1)(-\gamma - \lambda_2)$$

There are two solutions to this equation: $\lambda_1 = r$ and $\lambda_2 = -\gamma$. This means that the extinction equilibrium is a saddle point because it will be stable for P as long as $\gamma > 0$ but unstable for N as long as $r > 0$.

We now determine the stability of the N equilibrium $\left\{\hat{N} = K, \hat{P} = 0\right\}$:

$$\mathbf{J}(K,0) = \begin{bmatrix} -r & -\beta K \\ 0 & \delta K - \gamma \end{bmatrix}$$

Analyzing the more realistic model

The determinant of the jacobian yields the following characteristic polynomial:

$$0 = (-r - \lambda_1)(\delta K - \gamma - \lambda_2)$$

There are two solutions to this equation: $\lambda_1 = -r$ and $\lambda_2 = \delta K - \gamma$. This means that the N equilibrium will be stable as long as $\delta K < \gamma$ (i.e., predator mortality greater than maximum predator growth due to prey consumption).

We are now ready to analyze the interior equilibrium $\left\{\hat{N} = \frac{\gamma}{\delta}, \hat{P} = \frac{r}{\beta}\left(1 - \frac{\gamma}{\delta K}\right)\right\}$:

$$\mathbf{J}\left(\hat{N}, \hat{P}\right) = \begin{bmatrix} \frac{rK - 2r\frac{\gamma}{\delta} - Kr\left(1 - \frac{\gamma}{\delta K}\right)}{K} & -\beta\frac{\gamma}{\delta} \\ \frac{\delta r}{\beta}\left(1 - \frac{\gamma}{\delta K}\right) & 0 \end{bmatrix}$$

Analyzing the more realistic model

The determinant of the jacobian yields the following characteristic polynomial:

$$0 = \lambda^2 + \frac{r\gamma}{\delta K}\lambda + \frac{r\gamma}{\delta K}(\delta K - \gamma)$$

We solve for λ by using the quadratic formula with $a = 1$, $b = \frac{r\gamma}{\delta K}$ and $c = \frac{r\gamma}{\delta K}(\delta K - \gamma)$:

$$\lambda = \frac{-\frac{r\gamma}{\delta K} \pm \sqrt{\frac{r\gamma}{\delta K}\left(\frac{r\gamma}{\delta K} - 4(\delta K - \gamma)\right)}}{2}$$

This model is not **structurally unstable** as the interior equilibrium can have eigenvalues with non-zero real parts.

Indeed, the equilibrium will be stable as long as $K > \frac{\gamma}{\delta}$.

Analyzing the more realistic model

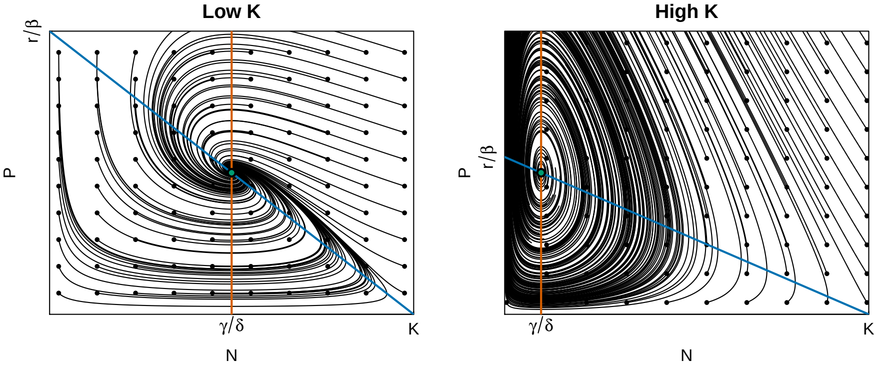
Because $K > \frac{\gamma}{\delta}$ is also the condition required for a biologically feasible equilibrium, we know that if the **equilibrium exists** it will necessarily be **stable**.

Hence, this shows that the predator-prey oscillations predicted by the Lotka-Volterra model are **not robust** to more realistic scenarios whereby the prey experiences **density-dependent growth or mortality**.

Overall, **density-dependence** in the prey thus **stabilizes** the interior equilibrium.

Graphically, this means that adding density-dependence in the prey prevents the ZNGI from being orthogonal.

Effect of density-dependence on interior equilibrium



The interior equilibrium is stable as long as it is feasible because density-dependence in the prey leads to non-orthogonal ZNGI that prevent oscillations from persisting.

The higher the carrying capacity K, the more orthogonal the ZNGI will be and the longer it will take for the oscillations to dampen.

Assumptions of the more realistic model

- **Logistic growth**: the prey species will experience density-dependence (logistic growth) due to intraspecific competition
- **Specialist predator**: the predator is a specialist that can only perist in the presence of the prey
- **Insatiable predator**: individual predators can consume an infinite number of prey
- **Constant parameters**: the model parameters do not vary over time due to demographic or environmental stochasticity
- **Random interactions**: individual predator encounter prey randomly in a homogeneous environment

References

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Volterra, V. 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris.