Dynamics of Two Species with Density-Dependent Interactions in a Mutualistic Context

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Modélisation Mathématique et Biodiversité

A Density-Dependent Interaction

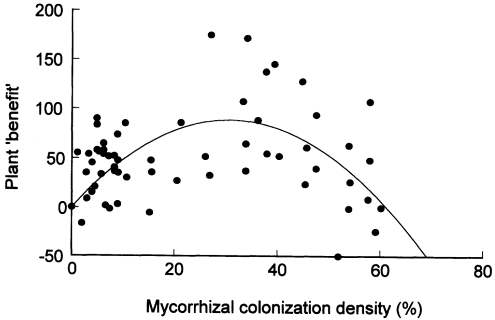


Figure 1: Experimental results and fitted curve showing the net benefit gained by plants with mycorrhizae in relation to their density[1].

- How do variations in **population density** affect the nature and intensity of mutualistic interactions?

[1] Gange and Ayres (1999)

Outline

Model Setup

Interaction Dynamics in Two Populations

Periodic Solutions of Mutualistic Models

Model

To consider the density of both populations x and y, we introduce[2]:

$$\begin{cases} \dot{x} & = x f(x, y) \\ \dot{y} & = y g(x, y) \end{cases} \quad (1)$$

We denote by Γ_f and Γ_g:

$$\Gamma_f := \{(x, y) \in \mathbb{R}_+ \times \mathbb{R}_+, f(x, y) = 0\}$$

and

$$\Gamma_g := \{(x, y) \in \mathbb{R}_+ \times \mathbb{R}_+, g(x, y) = 0\},$$

with $\Gamma_f \neq \emptyset$ and $\Gamma_g \neq \emptyset$.

[2] Brauer and Castillo-Chavez (2012), May (1972), Hale and Valdovinos (2021)

Examples

$$\begin{cases} \dot{x} = x\left(c_x - x - a_x(y - b_x)^2\right) r_x \\ \dot{y} = y\left(c_y - y - a_y(x - b_y)^2\right) r_y \end{cases}$$

(Zhang (2003))

$$\begin{cases} \dot{x} = x\left(\frac{K_x \gamma_{xy} y - x}{K_x + \gamma_{xy} y} - ay\right) r_x \\ \dot{y} = y\left(\frac{K_y + \alpha_{yx} x - y}{K_y}\right) r_y \end{cases}$$

(Neuhauser and al. (2004))

$$\begin{cases} \dot{x} = x(r_{x0} + (r_{x1} - r_{x0})(1 - \exp(-k_x y)) - a_x x) \\ \dot{y} = y(r_{y0} + (r_{y1} - r_{y0})(1 - \exp(-k_y x)) - a_y y) \end{cases}$$

(Graves and al. (2006))

$$\begin{cases} \dot{x} = x\left(r_x + c_x\left(\frac{a_{xy} y}{h_y + y}\right) - q_x\left(\frac{\beta_{xy} y}{e_x + x}\right) - s_x x\right) \\ \dot{y} = y\left(r_y + c_y\left(\frac{a_{yx} x}{h_x + x}\right) - q_y\left(\frac{\beta_{yx} x}{e_y + y}\right) - s_y y\right) \end{cases}$$

(Holland and DeAngelis (2010))

Key Assumptions

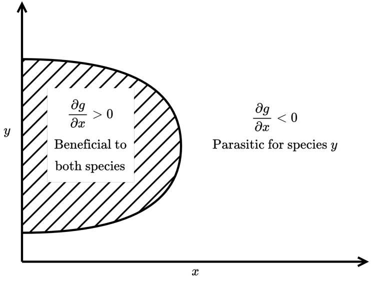
- **Mutualism and Parasitism**: $\frac{\partial f}{\partial y} > 0$ and $\frac{\partial g}{\partial x} > 0$ represent a region of strict mutualism. $\frac{\partial f}{\partial y} < 0$ or $\frac{\partial g}{\partial x} < 0$ represent a region of parasitism.
- **Intraspecific Competition**: $\frac{\partial f}{\partial x} < 0$ and $\frac{\partial g}{\partial y} < 0$ describe negative feedback within each species.
- **Intraspecific Cooperation**: $\frac{\partial f}{\partial x} > 0$ and $\frac{\partial g}{\partial y} > 0$ describe positive feedback within each species.
- **Dynamic Transitions**: The signs of $\frac{\partial f}{\partial y}$ and $\frac{\partial g}{\partial x}$ are not fixed and may change with species densities.

Mutualism

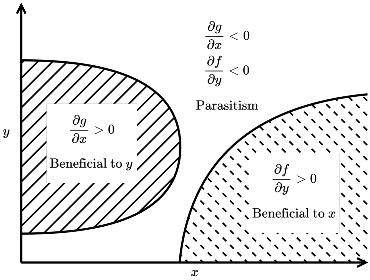
Definition 1

A system of differential equations of the form (1) will be said to be mutualistic if, in the phase portrait of $\mathbb{R}_+ \times \mathbb{R}_+$, there is *at least* a region where $\frac{\partial g}{\partial x} > 0$ and *at least* a region where $\frac{\partial f}{\partial y} > 0$. **These two regions may be disjoint.**

Examples



(a) Throughout the domain, $\frac{\partial f}{\partial y} > 0$.



(b) Non-overlapping mutualistic effects.

Figure 2: *Examples of strict mutualism and disjoint regions of mutualistic influence.* Strict mutualism occurs where both partial derivatives are positive and overlap.

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Hypothesis

Hypothesis H1

The functions f and g each define a single additional isocline, beyond those at $x = 0$ and $y = 0$: a vertical isocline for f and a horizontal isocline for g. The zeros (x, y) of f (resp. of g) form a single continuous curve.

Hypothesis H2

Γ_f and Γ_g delimit regions of strict constant sign of f and g. Moreover we impose that the signs of f (respectively of g) change on either side of the curve Γ_f (respectively of the curve Γ_g).

$$\begin{cases} \dot{x} & = xf(x,y) = x\Big(e_1 y - d_1\left((x-a_1)^{b_1} + c_1\right)\Big) \\ \dot{y} & = yg(x,y) = y\Big(e_2 x - d_2\left((y-a_2)^{b_2} + c_2\right)\Big) \end{cases} \quad (2)$$

with a_i, c_i, d_i, e_i positive constants, b_i positive integers.

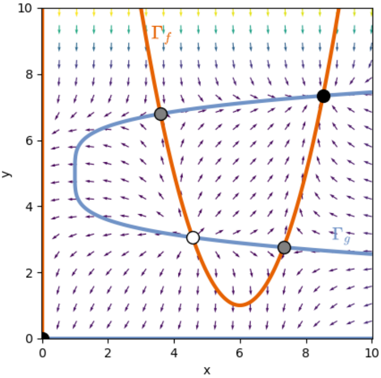


Figure 3: *Example of a mutualism model exhibiting different types of equilibrium points.* White points represent repulsive points, black points attractive points and gray points saddle points.

Hypothesis

Hypothesis H3

No more than two isoclines intersect at any given point.

In particular, H3 implies that $(0,0) \notin \Gamma_f \cup \Gamma_g$.

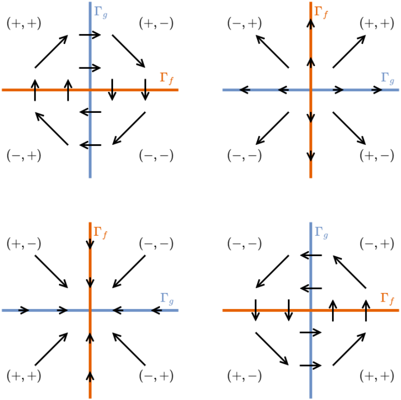
Hypothesis H4

We exclude the boundary cases where the equilibrium points are formed by two isoclines that only touch at that point but do not cross, and the case where the isoclines are coincident.

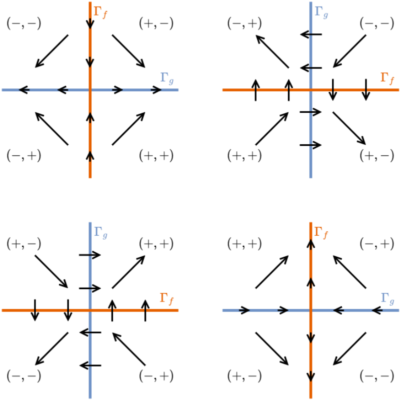
Alternating Fixed Points with Indices +1 and –1

Theorem 1

Let a dynamical system in $\mathbb{R}_+ \times \mathbb{R}_+$ be described by (1), with functions f and g satisfying hypotheses H1 to H4. Then, in the positive quadrant, the equilibrium points of the system alternate along the isoclines between having an index of $+1$ and an index of -1.

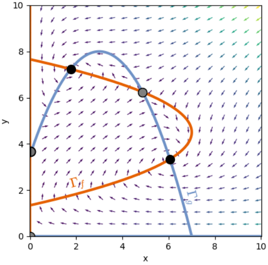


(a) Local structure of the phase portrait around an index $+1$ equilibrium.

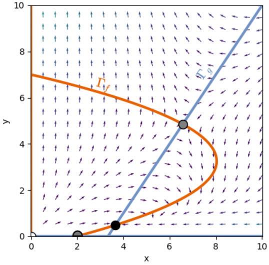


(b) Local structure of the phase portrait around an index -1 equilibrium.

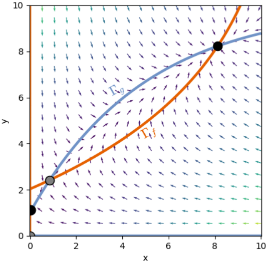
Figure 4: *Two possible local configurations of the phase portrait near an equilibrium point*, corresponding to the two admissible clockwise sign changes of the vector field across adjacent regions.



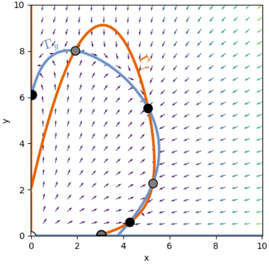
(a) Zhang (2003)



(b) Neuhauser and al. (2004)



(c) Graves and al. (2006)



(d) Holland and al. (2010)

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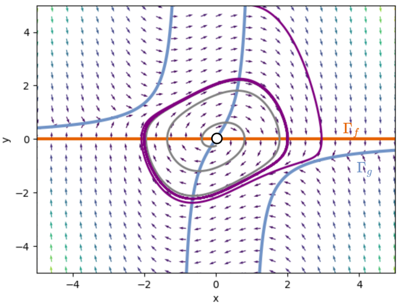
Limit Cycle and Center[3]

(a) Lotka–Volterra Center.



(b) Van der Pol Limit Cycle.

Figure 6: *Phase portraits illustrating two types of periodic dynamics.*

[3] May (1972)

No Limit Cycle in Strict Mutualism

Theorem 2

Let a dynamical system in $\mathbb{R}_+ \times \mathbb{R}_+$ be described by (1), with functions f and g satisfying hypotheses H1 to H4. We assume that the curves Γ_f and Γ_g intersect at ***a repulsive equilibrium point*** *(x^*, y^*), with $\frac{\partial f}{\partial y}(x^*, y^*) > 0$ and $\frac{\partial g}{\partial x}(x^*, y^*) > 0$. Then, there exists a region R in the phase portrait containing this point, in which the partial derivatives do not change sign, and no limit cycle exists that surrounds this point within R.*

Limit Cycle with Parasitism

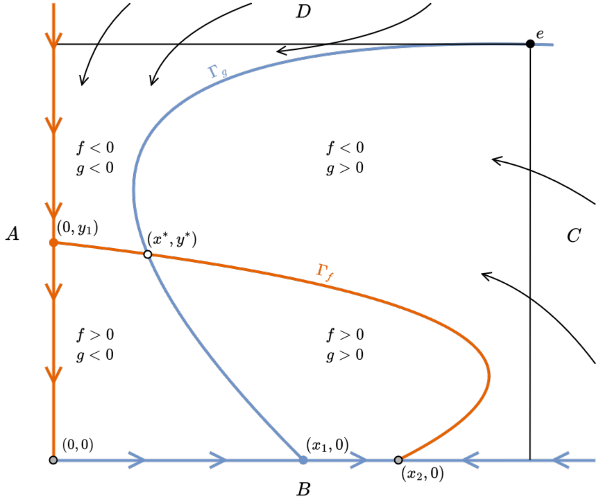


Figure 7: *Phase portrait assuming extended mutualism leading to a cyclic behaviour.*

Limit Cycle with Parasitism

Theorem 3

Let a dynamical system in $\mathbb{R}_+ \times \mathbb{R}_+$ be described by (1), with functions f and g satisfying conditions 1.1-1.10. Then a limit cycle exists inside the positive quadrant.

$$\begin{cases} \dot{x} & = x f(x,y) = x\left(a_1 - b_1 (y - c_1)^2 - d_1 x\right) \\ \dot{y} & = y g(x,y) = y\left(-a_2 - b_2 (y - c_2)^2 + d_2 x\right) \end{cases} \quad (3)$$

with (a_i, b_i, c_i, d_i) being positive constants.

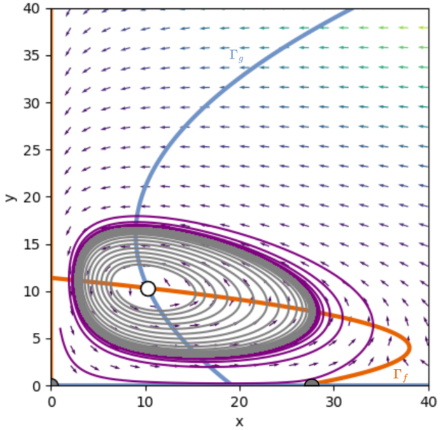


Figure 8: *Phase portrait leading to a limit cycle.*

Thank you for your attention

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Index Theory

$$\begin{cases} \dot{x} &= F(x, y) \\ \dot{y} &= G(x, y) \end{cases} \tag{4}$$

defines a vector field for which the slope:

$$\frac{dy}{dx} = \frac{G(x, y)}{F(x, y)} \tag{5}$$

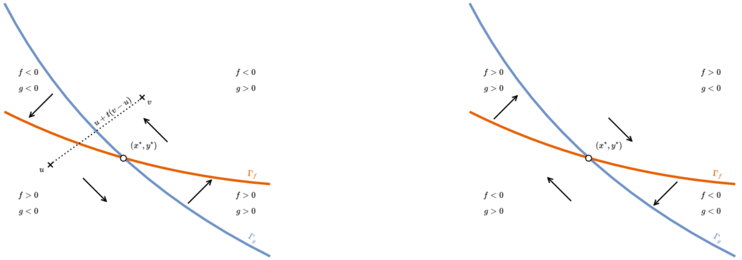
forms an angle with the x-axis given by:

$$\varphi(x, y) = \arctan\left(\frac{G(x, y)}{F(x, y)}\right). \tag{6}$$

Given this angle and a simple closed curve γ in $\mathbb{R}^2$, the index of γ , denoted $\text{Ind}(\gamma)$, is defined as:

$$\text{Ind}(\gamma) = \frac{1}{2\pi} \oint_\gamma d\varphi(x, y). \tag{7}$$

Proof of Theorem 2



(a) First possible alternation

(b) Second possible alternation

Figure 9: *Two possible neighborhoods of the repulsive equilibrium point* (x^*, y^*)

Let u and v be points as shown in Figure 9a, and define the function h as follows:

$$\begin{aligned} h : [0,1] &\to \mathbb{R} \\ t &\mapsto f(u + t(v-u)) \end{aligned}$$

No Limit Cycle in Strict Mutualism

Theorem 4

Let a dynamical system in $\mathbb{R}_+ \times \mathbb{R}_+$ be described by (1), with functions f and g satisfying hypotheses H1 to H4. We assume that the curves Γ_f and Γ_g intersect at ***an attractive equilibrium point*** *(x^*, y^*), with $\frac{\partial f}{\partial y}(x^*, y^*) > 0$ and $\frac{\partial g}{\partial x}(x^*, y^*) > 0$. Then, there exists a region R_2 in the phase portrait containing this point, in which the partial derivatives do not change sign, and no limit cycle exists that surrounds this point within R_2.*

Conditions 1.1-1.10 I

1.1 $\frac{\partial f}{\partial x} < 0$: Intraspecific competition.

1.2 $\frac{\partial g}{\partial y} > 0$ then $\frac{\partial g}{\partial y} < 0$: At low density, species y experiences self-cooperation rather than competition, then negative effects do emerge.

1.3 $\frac{\partial g}{\partial x} > 0$: Species x always has a positive effect on species y.

1.4 $\frac{\partial f}{\partial y} > 0$ then $\frac{\partial f}{\partial y} < 0$: At low density, species y has a positive effect on species x, then the interaction shifts from mutualism to parasitism.

1.5 $f(0, y_1) = 0$: Above the threshold y_1, the population of x declines, regardless of whether its own density is low or high.

1.6 $g(x_1, 0) = 0$: The threshold x_1 of species x required for species y to persist at low density.

Conditions 1.1-1.10 II

1.7 $f(x_2, 0) = 0$: There exists an equilibrium at x_2 where species x can persist in the absence of species y. Beyond x_2, the species x declines due to overpopulation.

1.8 $x_1 < x_2$: The threshold density for species x to persist in isolation (x_2) is higher than the threshold where species x can sustain y (x_1). Otherwise, species y goes extinct.

1.9 (x^*, y^*) is a repulsive equilibrium point:

$$x^* \frac{\partial f}{\partial x}(x^*, y^*) + y^* \frac{\partial g}{\partial y}(x^*, y^*) > 0,$$

and

$$x^* y^* \left(\frac{\partial f}{\partial x}(x^*, y^*) \frac{\partial g}{\partial y}(x^*, y^*) - \frac{\partial f}{\partial y}(x^*, y^*) \frac{\partial g}{\partial x}(x^*, y^*) \right) > 0.$$

Conditions 1.1-1.10 III

This condition ensures that small perturbations around (x^*, y^*) will lead to divergence, favoring oscillatory or cyclic behavior.

1.10 The isoclines $f = 0$ and $g = 0$ have the shapes illustrated in Figure 7.

Conditions 2.1-2.9 I

2.1 $\frac{\partial g}{\partial y} < 0$: Intraspecific competition for species y.

2.2 $\frac{\partial f}{\partial x} > 0$ then $\frac{\partial f}{\partial x} < 0$: At low density, species x experiences self-cooperation rather than competition, then negative effects emerge.

2.3 $\frac{\partial f}{\partial y} > 0$: Species y always has a positive effect on species x.

2.4 $\frac{\partial g}{\partial x} < 0$ then $\frac{\partial g}{\partial x} > 0$: At low density, species x has a negative effect on species y, but as its density increases, the interaction shifts from parasitism to mutualism.

2.5 $f(0, y_1) = 0$: Beyond the threshold y_1, the population of x grows due to mutualism, regardless of its own density.

2.6 $g(0, y_2) = 0$: There exists an equilibrium at y_2 where species y can persist in the absence of species x. Beyond y_2, the species y declines due to overpopulation.

Conditions 2.1-2.9 II

2.7 $y_1 < y_2$: The threshold density for species y to persist in isolation (y_2) is higher than the threshold where species y can sustain x (y_1). Otherwise, species x goes extinct.

2.8 (x^*, y^*) is a repulsive equilibrium point.

2.9 The isoclines $f = 0$ and $g = 0$ have the shapes illustrated in Figure 10.

Limit Cycle with Parasitism

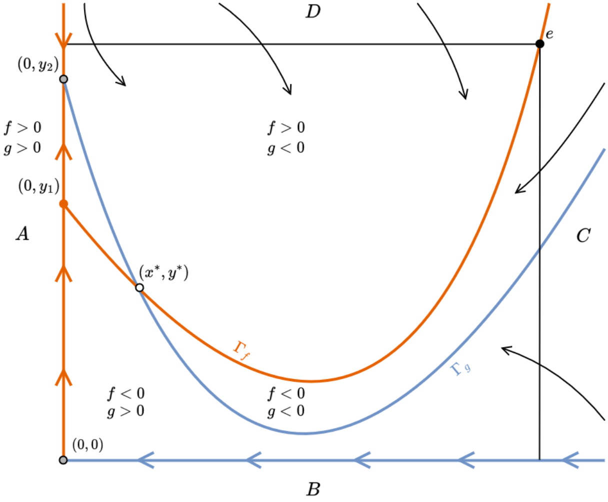


Figure 10: *Phase portrait assuming extended mutualism leading to a cyclic behaviour.*

Limit Cycle with Parasitism

Theorem 5

Let a dynamical system in $\mathbb{R}_+ \times \mathbb{R}_+$ be described by (1), with functions f and g satisfying conditions 2.1-2.10. Then a cycle limit exists inside the positive quadrant.