Population Dynamics with Space

qazxwecvr

Abstract

There are many models describing population dynamics in terms of total numbers or densities in the modeled habitat. One such model is the Lotka-Volterra Equations. Here, I specify a simple extension of this model that describes population densities distributed over a given space. Organisms with the same position interact according to the Lotka-Volterra model, and organisms have the ability to move to more favorable locations. Compounding forces are simply combined additively.

1 Food Chain

The basic case will consist of a number N of species, each with an index n where $N \geq n \geq 1$. Species n will predate on the species $n-1$, and species 1 will predate on no species, with each organism receiving a constant amount of energy from some unspecified source. Species N will have no predator. Each species will breed. Each species may move according to two goals: seeking food and avoiding predators. Movement and interactions between organisms at the same position will be discussed separately, and then combined into a full equation describing the full behavior of the food chain. $T_n(\mathcal{R}, t)$ is the total population of species n in region $\mathcal{R}$ at time t.

1.1 Same-Position Interaction

Organisms at the same position will interact with each other. They may breed, predate, and die. These interactions will be discussed here in isolation. The model for these interactions will be based on the Lotka-Volterra equations. Using information from Wikipedia, a form of the Lotka-Volterra equations can be fit to the model here for $N = 2$ as follows:

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 \mathrm{P}_2$$
$$\frac{\partial \mathrm{P}_2}{\partial t} = b_2 \mathrm{P}_1 \mathrm{P}_2 - d_2 \mathrm{P}_2$$

Here, total population has been replaced with the population density at $\vec{x}$. This model will add the restriction $b_n, d_n \geq 0$ for any n. These equations can be used to form the special cases of species 1 and N, becoming:

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 \mathrm{P}_2$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = b_N \mathrm{P}_{N-1} \mathrm{P}_N - d_N \mathrm{P}_N$$

for $N > 1$. If $N = 1$, the following combination of the equations, which selects the terms that describe breeding and death independent on another species, can be used to describe the system:

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 = \mathrm{P}_1(b_1 - d_1)$$

To find the equations of a species with an index between 1 and N, another combination of the equations can be used that selects the terms that describe breeding and death dependent on another species:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1} \mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1}$$

1.2 Summary

Equation for $N = 1$:

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 = \mathrm{P}_1(b_1 - d_1)$$

System for $N > 1$:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1} \mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1}$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 \mathrm{P}_2$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = b_N \mathrm{P}_{N-1} \mathrm{P}_N - d_N \mathrm{P}_N$$

Where the first equation applies for each species n for $N > n > 1$.

1.3 Movement

Movement will be discussed here in isolation. With movement alone controlling organisms, the populations will be conserved, since there is no birth or death. Therefore, the population distributions can be described with a continuity equation of the form:

$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \vec{\mathrm{F}}_n$$

where $\vec{\mathrm{F}}_n(\vec{x}, t)$ is the flux of the population of species n. The flux at a point is equal to the velocity of the organisms at that point times the density at that point:

$$\vec{\mathrm{F}}_n = \mathrm{P}_n \vec{\mathrm{V}}_n$$

where $\vec{\mathrm{V}}_n$ is the velocity of the organisms. The movement velocity is determined by a taking into account the two factors mentioned above; organisms flee their predators and seek their prey. The organisms will seek their prey by traveling in the direction in which the prey density increases the most quickly, so one part of $\vec{\mathrm{V}}_n$ is:

$$\beta_n \nabla \mathrm{P}_{n-1}$$

where $\beta_n \geq 0$ is the "strength" of the urge to seek food. Similarly organisms will flee their predators by traveling in the direction in which the predator density decreases the most quickly, so another part of $\vec{\mathrm{V}}_n$ is:

$$-\delta_n \nabla \mathrm{P}_{n+1}$$

where $\delta_n \geq 0$. To combine these to goals into a complete $\vec{\mathrm{V}}_n$, they can be added together to create the linear combination:

$$\vec{\mathrm{V}}_n = \beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}$$

Species without predators or prey will have the predator and prey term excluded, respectively, so:

$$\vec{\mathrm{V}}_1 = -\delta_1 \nabla \mathrm{P}_2$$
$$\vec{\mathrm{V}}_N = \beta_N \nabla \mathrm{P}_{N-1}$$

as long as $N > 1$. If $N = 1$, the sole species has no predator or prey to effect movement, so the organisms do not move. The pieces defined so far can be combined into a full movement equation:

$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_n \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1} \big) \Big)$$

Simplifying (perhaps):

$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_n \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1} \big) \Big)$$
$$\frac{\partial \mathrm{P}_n}{\partial t} = -\Big(\nabla \mathrm{P}_n \cdot \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1} \big) + \mathrm{P}_n \nabla \cdot \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1} \big) \Big)$$
$$\frac{\partial \mathrm{P}_n}{\partial t} = \nabla \mathrm{P}_n \cdot \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1} \big) - \mathrm{P}_n \big(\beta_n \nabla^2 \mathrm{P}_{n-1} - \delta_n \nabla^2 \mathrm{P}_{n+1} \big)$$

One can alternatively keep the predator and prey terms separate:

$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_n \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1} \big) \Big)$$
$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \big(\mathrm{P}_n \beta_n \nabla \mathrm{P}_{n-1} - \mathrm{P}_n \delta_n \nabla \mathrm{P}_{n+1} \big) \big)$$
$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \big(\mathrm{P}_n \beta_n \nabla \mathrm{P}_{n-1} \big) + \nabla \cdot \big(\mathrm{P}_n \delta_n \nabla \mathrm{P}_{n+1} \big)$$
$$\frac{\partial \mathrm{P}_n}{\partial t} = -\beta_n \nabla \cdot \big(\mathrm{P}_n \nabla \mathrm{P}_{n-1} \big) + \delta_n \nabla \cdot \big(\mathrm{P}_n \nabla \mathrm{P}_{n+1} \big)$$
$$\frac{\partial \mathrm{P}_n}{\partial t} = -\beta_n \big(\nabla \mathrm{P}_n \cdot \nabla \mathrm{P}_{n-1} + \mathrm{P}_n \nabla^2 \mathrm{P}_{n-1} \big) + \delta_n \big(\nabla \mathrm{P}_n \cdot \nabla \mathrm{P}_{n+1} + \mathrm{P}_n \nabla^2 \mathrm{P}_{n+1} \big)$$

The special case of species 1:

$$\frac{\partial \mathrm{P}_1}{\partial t} = -\nabla \cdot \big(\mathrm{P}_1 \vec{\mathrm{V}}_1 \big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_1 \big(-\delta_1 \nabla \mathrm{P}_2 \big) \Big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = \delta_1 \nabla \cdot \big(\mathrm{P}_1 \nabla \mathrm{P}_2 \big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = \delta_1 \big(\nabla \mathrm{P}_1 \cdot \nabla \mathrm{P}_2 + \mathrm{P}_1 \nabla^2 \mathrm{P}_2 \big)$$

The special case of species N:

$$\frac{\partial \mathrm{P}_N}{\partial t} = -\nabla \cdot \left(\mathrm{P}_N \vec{\mathrm{V}}_N\right)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_N \left(\beta_N \nabla \mathrm{P}_{N-1}\right)\Big)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = -\beta_N \nabla \cdot \left(\mathrm{P}_N \nabla \mathrm{P}_{N-1}\right)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = -\beta_N \left(\nabla \mathrm{P}_N \cdot \nabla \mathrm{P}_{N-1} + \mathrm{P}_N \nabla^2 \mathrm{P}_{N-1}\right)$$

1.3.1 Summary

Equation for $N = 1$:

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 = \mathrm{P}_1 (b_1 - d_1)$$

System for $N > 1$:

$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_n \left(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}\right)\Big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = \delta_1 \left(\nabla \mathrm{P}_1 \cdot \nabla \mathrm{P}_2 + \mathrm{P}_1 \nabla^2 \mathrm{P}_2\right)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = -\beta_N \left(\nabla \mathrm{P}_N \cdot \nabla \mathrm{P}_{N-1} + \mathrm{P}_N \nabla^2 \mathrm{P}_{N-1}\right)$$

Where the first equation applies for each species n for $N > n > 1$. Using shorter forms of the equations for the special cases:

$$\frac{\partial \mathrm{P}_n}{\partial t} = -\nabla \cdot \Big(\mathrm{P}_n \left(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}\right)\Big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = \delta_1 \nabla \cdot \left(\mathrm{P}_1 \nabla \mathrm{P}_2\right)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = -\beta_N \nabla \cdot \left(\mathrm{P}_N \nabla \mathrm{P}_{N-1}\right)$$

1.4 Full Model

To combine the two pieces of the model, a more general continuity equation can be used:

$$\frac{\partial \mathrm{P}_n}{\partial t} = \mathrm{S}_n - \nabla \cdot \vec{\mathrm{F}}_n$$

Where $\mathrm{S}_n(\vec{x}, t)$ describes the rate at which organisms are being born and dying at $\vec{x}$ at time t. This was described in section 1.1, so the results formulated there will be used to determine S_n. For example, one equation from that section is:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1} \mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1}$$

The rate at which the organisms are being born and dying in the above equation ($\frac{\partial \mathrm{P}_n}{\partial t}$) can be substituted for S_n:

$$\mathrm{S}_n = b_n \mathrm{P}_{n-1} \mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1}$$

Substituting this into the continuity equation:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1}\mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1} - \nabla \cdot \vec{\mathrm{F}}_n$$

Expanding this into a fuller equation:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1}\mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1} - \nabla \cdot \Big(\mathrm{P}_n \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}\big)\Big)$$

Summary Equation for $N = 1$:

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 = \mathrm{P}_1 (b_1 - d_1)$$

System for $N > 1$:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1}\mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1} - \nabla \cdot \Big(\mathrm{P}_n \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}\big)\Big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 \mathrm{P}_2 + \delta_1 \big(\nabla \mathrm{P}_1 \cdot \nabla \mathrm{P}_2 + \mathrm{P}_1 \nabla^2 \mathrm{P}_2\big)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = b_N \mathrm{P}_{N-1}\mathrm{P}_N - d_N \mathrm{P}_N - \beta_N \big(\nabla \mathrm{P}_N \cdot \nabla \mathrm{P}_{N-1} + \mathrm{P}_N \nabla^2 \mathrm{P}_{N-1}\big)$$

Where the first equation applies for each species n for $N > n > 1$. Using shorter forms of the equations for the special cases:

$$\frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_{n-1}\mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1} - \nabla \cdot \Big(\mathrm{P}_n \big(\beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}\big)\Big)$$
$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1 \mathrm{P}_1 - d_1 \mathrm{P}_1 \mathrm{P}_2 + \delta_1 \nabla \cdot \big(\mathrm{P}_1 \nabla \mathrm{P}_2\big)$$
$$\frac{\partial \mathrm{P}_N}{\partial t} = b_N \mathrm{P}_{N-1}\mathrm{P}_N - d_N \mathrm{P}_N - \beta_N \nabla \cdot \big(\mathrm{P}_N \nabla \mathrm{P}_{N-1}\big)$$

2 Food Web

Here, the model above for a food chain will be extended to arbitrary food webs. A food web will again contain N species, each with an index n such that $N \geq n \geq 1$. Unlike the food chain model, however, the index of the species will not determine its predators and prey. Instead, each species will have a set of predator species D_n and a set of prey species B_n. These sets will contain the indices of the pretator and prey species of species n, respectively. Note the following relationship:

$$B_n = \{x | n \in D_x\}$$
$$D_n = \{x | n \in B_x\}$$

The fundamental continuity equation from the food chain model can be written:

$$\frac{\partial \mathrm{P}_n}{\partial t} = \mathrm{S}_n - \nabla \cdot (\mathrm{P}_n \vec{\mathrm{V}}_n)$$

This can be used, with altered definitions of S_n and $\vec{\mathrm{V}}_n$.

2.1 Same-Position Interaction

The definition of S_n for the normal case was:

$$\mathrm{S}_n = b_n \mathrm{P}_{n-1} \mathrm{P}_n - d_1 \mathrm{P}_n \mathrm{P}_{n+1}$$

The food web model needs to combine the multiple possible predator and prey species' effects. For this model, each other species in the equation will have its own coefficient. For example, $b_{n,i}$ will be the coefficient found in the term for species i in the equation for species n. The effects of each other species will simply be summed, resulting in the following definition for S_n:

$$\mathrm{S}_n = \sum_{i \in B_n} b_{n,i} \mathrm{P}_n \mathrm{P}_i - \sum_{i \in D_n} d_{n,i} \mathrm{P}_n \mathrm{P}_i$$

For the special cases, i.e. a species with an empty predator or prey set, the corresponding terms will be replaced with the simpler alternatives that depend only on the species itself:

$$\begin{aligned}
B_n = \varnothing \quad & \Longrightarrow \mathrm{S}_n = b_n \mathrm{P}_n - \sum_{i \in D_n} d_{n,i} \mathrm{P}_n \mathrm{P}_i \\
D_n = \varnothing \quad & \Longrightarrow \mathrm{S}_n = \sum_{i \in B_n} b_{n,i} \mathrm{P}_n \mathrm{P}_i - d_n \mathrm{P}_n \\
B_n, D_n = \varnothing \quad & \Longrightarrow \mathrm{S}_n = \mathrm{P}_n (b_n - d_n)
\end{aligned}$$

2.2 Movement

The movement term can be modified similarly. The food chain definition of $\vec{\mathrm{V}}_n$:

$$\vec{\mathrm{V}}_n = \beta_n \nabla \mathrm{P}_{n-1} - \delta_n \nabla \mathrm{P}_{n+1}$$

Like before, predator and prey species will have its own constant and the effects of the species will be summed:

$$\vec{\mathrm{V}}_n = \sum_{i \in B_n} \beta_{n,i} \nabla \mathrm{P}_i - \sum_{i \in D_n} \delta_{n,i} \nabla \mathrm{P}_i$$

When a species has no predator or prey, there is no need for a predator or prey term. The above formula will work for these cases, since B_n and D_n will be $\varnothing$. This formula can be used to form the full movement term:

$$-\nabla \cdot \left(\mathrm{P}_n \Big(\sum_{i \in B_n} \beta_{n,i} \nabla \mathrm{P}_i - \sum_{i \in D_n} \delta_{n,i} \nabla \mathrm{P}_i \Big) \right)$$

although one may wish to simplify the relevant terms out in these cases.

2.3 Full Model

$$B_n, D_n \neq \varnothing \implies \begin{aligned} \frac{\partial \mathrm{P}_n}{\partial t} &= \sum_{i \in B_n} b_{n,i} \mathrm{P}_n \mathrm{P}_i - \sum_{i \in D_n} d_{n,i} \mathrm{P}_n \mathrm{P}_i \\ &\quad - \nabla \cdot \left(\mathrm{P}_n \Big(\sum_{i \in B_n} \beta_{n,i} \nabla \mathrm{P}_i - \sum_{i \in D_n} \delta_{n,i} \nabla \mathrm{P}_i \Big) \right) \end{aligned}$$

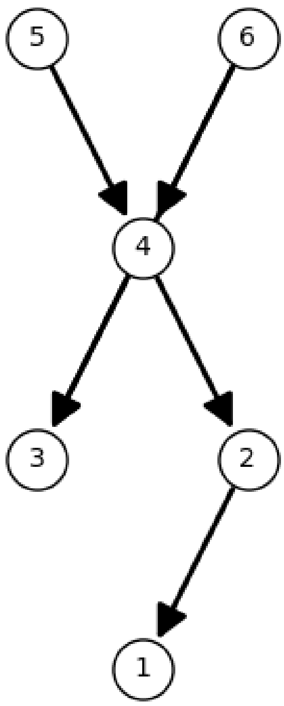
$$B_n = \varnothing \implies \frac{\partial \mathrm{P}_n}{\partial t} = b_n \mathrm{P}_n - \sum_{i \in D_n} d_{n,i} \mathrm{P}_n \mathrm{P}_i + \nabla \cdot \left(\mathrm{P}_n \sum_{i \in D_n} \delta_{n,i} \nabla \mathrm{P}_i \right)$$

$$D_n = \varnothing \implies \frac{\partial \mathrm{P}_n}{\partial t} = \sum_{i \in B_n} b_{n,i} \mathrm{P}_n \mathrm{P}_i - d_n \mathrm{P}_n - \nabla \cdot \left(\mathrm{P}_n \sum_{i \in B_n} \beta_{n,i} \nabla \mathrm{P}_i \right)$$

$$B_n, D_n = \varnothing \implies \frac{\partial \mathrm{P}_n}{\partial t} = \mathrm{P}_n (b_n - d_n)$$

2.4 Example

This food web will be used as an example:



The food web can be described with the following sets:

$$B_6 = \{4\} \qquad B_5 = \{4\}$$
$$D_6 = \varnothing \qquad D_5 = \varnothing$$

$$B_4 = \{2,3\} \qquad B_3 = \varnothing$$
$$D_4 = \{5,6\} \qquad D_3 = \{4\}$$

$$B_2 = \{1\} \qquad B_1 = \varnothing$$
$$D_2 = \{4\} \qquad D_1 = \{2\}$$

Using these and the formulas given above, a complete system of equations for this food web can be created:

$$\frac{\partial \mathrm{P}_6}{\partial t} = b_{6,4}\mathrm{P}_6\mathrm{P}_4 - d_6\mathrm{P}_6 - \nabla \cdot \big(\mathrm{P}_6\beta_{6,4}\nabla\mathrm{P}_4\big)$$

$$\frac{\partial \mathrm{P}_5}{\partial t} = b_{5,4}\mathrm{P}_6\mathrm{P}_4 - d_5\mathrm{P}_5 - \nabla \cdot \big(\mathrm{P}_5\beta_{5,4}\nabla\mathrm{P}_4\big)$$

$$\frac{\partial \mathrm{P}_4}{\partial t} = b_{4,2}\mathrm{P}_4\mathrm{P}_2 + b_{4,3}\mathrm{P}_4\mathrm{P}_3 - (d_{4,5}\mathrm{P}_4\mathrm{P}_5 + d_{4,6}\mathrm{P}_4\mathrm{P}_6)$$
$$- \nabla \cdot \Bigg(\mathrm{P}_4\Big(\beta_{4,2}\nabla\mathrm{P}_2 + \beta_{4,3}\nabla\mathrm{P}_3 - \big(\delta_{4,5}\nabla\mathrm{P}_5 + \delta_{4,6}\nabla\mathrm{P}_6\big)\Big)\Bigg)$$

$$\frac{\partial \mathrm{P}_3}{\partial t} = b_3\mathrm{P}_3 - d_{3,4}\mathrm{P}_3\mathrm{P}_4 + \nabla \cdot \big(\mathrm{P}_3\delta_{3,4}\nabla\mathrm{P}_4\big)$$

$$\frac{\partial \mathrm{P}_2}{\partial t} = b_{2,1}\mathrm{P}_2\mathrm{P}_1 - d_{2,4}\mathrm{P}_2\mathrm{P}_4 - \nabla \cdot \Big(\mathrm{P}_2\big(\beta_{2,1}\nabla\mathrm{P}_1 - \delta_{2,4}\nabla\mathrm{P}_4\big)\Big)$$

$$\frac{\partial \mathrm{P}_1}{\partial t} = b_1\mathrm{P}_1 - d_{1,2}\mathrm{P}_1\mathrm{P}_2 + \nabla \cdot \big(\mathrm{P}_1\delta_{1,2}\nabla\mathrm{P}_2\big)$$