

### 10.3 Case studies that can be selected

#### 10.3.1.1 Case I: Including handling time in the hare-lynx system

In Tutorial 5, you studied the hare-lynx system, which could be described by a Lotka-Volterra predator-prey model. Several assumptions underly this particular model formulation, in particular regarding the predation term. Specifically, the predation term was modelled as:  $c_{12}HP$  (dimensions: number of prey per time). From this term, we can derive the consumption behavior of one individual predator (dimension: number of prey per predator per time). For the standard model that we used previously for the hare-lynx system, this was a linear function, which just kept increasing when the number of prey increased. However, this assumption may not be realistic, especially under circumstances when the prey density is already high: at some point, there may be a physiological limit to how much a predator can eat. For example, digesting the biomass of one prey takes time and energy, which is not spent hunting for additional prey. In other words, there is a handling time associated with the consumption of each prey, which will also limit the maximum number of prey that a predator can consume within a certain timeframe.



*Figure 9.9: A lynx digesting a recent meal. The time and energy spent digesting prey biomass is referred to as 'handling time'. Handling time was not considered in the models of Tutorial 5; this assignment will explore the consequences of including handling time for the emergent model dynamics.*

In this case study, you will modify the predation term in the hare-lynx model that was previously studied in class. Specifically, you will explain how the predation term needs to be rewritten (mathematically) to account for handling time, and subsequently analyze how this modification affects the behavior of the model system. As done for the other population models studied in class, this analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits.

### 10.3.1.2 Background for Case I

The Hare-Lynx model that was studied in Tutorial 5 can be viewed as one specific version of a more general predator-prey model:

$$\frac{dH}{dt} = rH - f(H)P \quad (12)$$

$$\frac{dP}{dt} = ef(H)P - dP \quad (13)$$

Where  $f(H)$  is a function that describes the predation rate for one individual predator, also referred to as the *per capita predation rate*. In the Tutorial, we assumed for this function:

$$f(H) = c_{12}H \quad (14)$$

Where the parameter  $c_{12}$  was a constant. As a result, the per capita predation rate was a linearly increasing function of prey availability: if the prey would double, then the predation rate of each individual predator would double as well. This assumption seems reasonable, as long as prey availability is very low. However, if the prey availability is already very high, then there may be physical limitation of how much one predator can eat, due to the handling time of each prey as described in the previous paragraph. We call this maximum per capita predation rate  $c_{max}$  (note that this  $c_{max}$  has different dimensions and units than the parameter  $c_{12}$  in the Hare-Lynx model of Tutorial 5!). So, we want to obtain a new function for  $f(H)$  that includes these two characteristics:

$$f(H = \text{small}) \approx cH \quad (15)$$

$$f(H = \text{large}) \approx c_{max} \quad (16)$$

You can verify yourself that the following function fulfills these two requirements:

$$f(H) = \frac{c_{max}H}{b+H} \quad (17)$$

Note that this function also introduces a new parameter  $b$ . As this parameter is added to the state variable  $H$ , we know that these two system components need to have the same dimensions and units. To see how this new function differs from the original function that was used in Tutorial 5, it is very insightful to plot both these functions in a plot that varies  $H$  on the x-axis, and that shows the corresponding value of  $f(H)$  on the y-axis. Inserting equation (17) into equations (12) and (13) then yields the model that includes the handling time. An interesting starting point for your analysis may be to consider the following set of parameter values:

$$\begin{aligned} r &= 0.2 & b &= 2400 \\ d &= 0.04 & c_{max} &= 0.2 \\ e &= 0.2 \end{aligned}$$

### 10.3.2.1 Case II: Including handling time and search success in the hare-lynx system

In Tutorial 5, you studied the hare-lynx system, which could be described by a Lotka-Volterra predator-prey model. Several assumptions underly this particular model formulation, in particular regarding the predation term. Specifically, the predation term was modelled as:  $c_{12}HP$  (dimension: number of prey per time). From this term, we can derive the consumption behavior of one individual predator (dimension: number of prey per predator per time). For the standard model that we used previously for the hare-lynx system, this was a linear function, which just kept increasing when the number of prey increased. However, this assumption may not be realistic under circumstances when the prey density is already high: at some point, there may be a physiological limit to how much a predator can eat. For example, digesting the biomass of one prey takes time and energy, which is not spent hunting for additional prey. In other words, there is a handling time associated with the consumption of each prey, which will also limit the maximum number of prey that a predator can consume within a certain timeframe. Moreover, the assumption of linearity may not be realistic at low densities of prey either. Predators develop a search image when they are hunting for prey, meaning that the more often they encounter a particular prey species, the better they become at recognizing this prey. In contrast, if a prey species is encountered only rarely, it decreases the ability of the predator to recognize it. Thus, at low prey densities, it may become more difficult for the predator to notice this prey.



*Figure 9.10: Like many other prey species, the snowshoe hare is well camouflaged within its natural environment. When the species is only rarely encountered, it becomes more difficult to recognize it. This phenomenon is referred to as the predator developing a search image, which requires learning from the experience of encountering the prey species. Developing a search image (and handling time of prey species) were not considered in the models of Tutorial 5; this assignment will explore the consequences of these processes for the emergent model dynamics.*

In this case study, you will modify the predation term in the hare-lynx model that was previously studied in class. Specifically, you will explain how the predation term needs to be rewritten (mathematically) to account for handling time (at high prey densities) and the lack of a search image (at low prey densities). Subsequently, you will analyze how this modification affects the behavior of the model system. As done for the other population models studied in class, this analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits.

### 10.3.2.2 Background for Case II

The Hare-Lynx model that was studied in Tutorial 5 can be viewed as one specific version of a more general predator-prey model:

$$\frac{dH}{dt} = rH - f(H)P \quad (18)$$

$$\frac{dP}{dt} = ef(H)P - dP \quad (19)$$

Where  $f(H)$  is a function that describes the predation rate for one individual predator, also referred to as the *per capita predation rate*. In the Tutorial, we assumed for this function:

$$f(H) = c_{12}H \quad (20)$$

In the background for Case I, you can read how this function can be adjusted to include the handling time of prey in the predation function. This yields a new function  $f(H)$  that can be written as:

$$f(H) = \frac{c_{max}H}{b+H} \quad (21)$$

This function increases almost linearly when the availability of prey,  $H$ , is small. If we compare a linear function to a quadratic function, then the latter increases more slowly at small values. Quadratic functions also increase more rapidly at larger values, but if we square both the numerator and the denominator of equation (21), we will again have a function approaching the maximum per capita predation rate  $c_{max}$ :

$$f(H) = \frac{c_{max}H^2}{b^2+H^2} \quad (22)$$

To see how this new function differs from the original function that was used in Tutorial 5, and the function used in Case I, it is very insightful to plot both these functions in a plot that varies  $H$  on the x-axis, and that shows the corresponding values of the three  $f(H)$  functions on the y-axis. Inserting equation (22) into equations (18) and (19) then yields the model that includes the handling time and the searching behavior at low densities. A possible starting point for this model is to use the following parameters:

$$r = 0.2 \quad b = 2400$$

$$d = 0.04 \quad e = 0.2$$

And see how the model behaves for different values of the maximum per capita predation rate (e.g. comparing  $c_{max} = 0.3$ ,  $c_{max} = 0.4$  and  $c_{max} = 0.5$ ). You can analyze the numerical dynamics, and create the corresponding state space portraits of these cases to explain the different dynamics that you may observed in this Case.

### 10.3.3.1 Case III: Modelling a food chain system

In Tutorial 5, you studied the hare-lynx system, which could be described by a Lotka-Volterra predator-prey model. In the tutorial, you assumed that the hare population could grow exponentially, only being limited by predation. This implicitly assumes that food supply is never a limiting factor for the hare. We have already seen that food limitation can be taken into account by including a crowding or self-limitation term in the model equation describing the prey population (as was done for the buffalo population in Tutorial 5). An alternative approach is to model the food source for the prey explicitly. In the hare-lynx system, the main food source of hares is grass, which is also self-limiting (as it competes with itself for space) and it is also consumed by hares.

How fast the grass can grow depends on site-specific conditions such as soil fertility and climate. These characteristics may not only affect the grass itself, but also lead to affects higher up in the food chain (i.e. affecting the hare or even the lynx population).

*Figure 9.11: In the predator-prey models of Tutorial 5, we considered that the growth rate of the prey population was a fixed parameter. However, the prey species themselves consume resources themselves; for example, the hares in the hare-lynx system are herbivores consuming mainly grasses. In this assignment, we consider a food chain model of three state variables, meaning that growth of the hares depends on consumption of grass, which is modelled as a separate state variable. This allows for considering different climatic conditions (leading to different growth rates of the grass).*



In this case study, you will extend the hare-lynx model by adding another differential equation, describing the dynamics of grass that is the main food source of the hares. It is advisable to first study how differential growth rates of the grass (representing different climatic conditions, for example), affect the dynamics in a two-tiered system (i.e. only grass and hares). Once you understand how this works, you can hypothesize what will happen when the predator is added to the system, and check with model simulations and analytical analyses whether your hypothesis is correct. As done for the other population models studied in class, your analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits. Because you now have three differential equations in the extended model, the state space becomes three-dimensional as well. You can still analyze two-dimensional state spaces (keeping the third state variable constant), and you can also make three-dimensional state space portraits using Matlab.

### 10.3.3.2 Background for Case III

In Tutorial 5, the hare-lynx system was modelled using the following differential equations:

$$\frac{dH}{dt} = rH - c_{12}HP \quad (23)$$

$$\frac{dP}{dt} = e c_{12}HP - dP \quad (24)$$

We can then include grass dynamics explicitly by introducing a new equation for grass:

$$\frac{dG}{dt} = r_G G - c_{GG}GG - c_{GH}GH \quad (25)$$

Where the last term is the consumption of grass by the hare, which then becomes the growth term for the hare. Thus, this means that the equation describing hare dynamics changes to:

$$\frac{dH}{dt} = e_{GH}c_{GH}GH - c_{HP}HP - d_H H \quad (26)$$

Where we also include a mortality term for the hare, which is needed if we want to study the two-component system (only grass and hares) first. Note that for the lynx equation, we need to make it clear that we have different efficiency and mortality parameters in that equation, which we can clarify if we use the following notation:

$$\frac{dP}{dt} = e_{HP}c_{HP}HP - d_P P \quad (27)$$

The two-component system is then described by equations (25) and (26) and the full food chain of three components by equations (25), (26) and (27). A possible starting point for the analysis is to consider the following parameter set:

$$\begin{aligned} c_{GG} &= 0.0002 & c_{GH} &= 0.002 \\ e_{GH} &= 0.2 & c_{HP} &= 0.002 & d_H &= 0.02 \\ e_{HP} &= 0.2 & d_P &= 0.04 \end{aligned}$$

And vary parameter  $r_G$  over a very large range of values, mimicking very low productive systems ( $r_G = 0.005$ ), up to very productive systems ( $r_G = 0.5$ ).

#### 10.3.4 Case IV: Including handling time in the lion-buffalo system

In Tutorial 5, you studied the lion-buffalo system, which could be described by a Lotka-Volterra predator-prey model that included a self-limitation/crowding term in the differential equation describing prey (i.e. buffalo) dynamics. Several assumptions underly this particular model formulation, in particular regarding the predation term. Specifically, the predation term was modelled as:  $c_{12}BL$  (dimension: number of prey per time). From this term, we can derive the consumption behavior of one individual predator (dimension: number of prey per predator per time). For the standard model that we used previously for the lion-buffalo system, this was a linear function, which just kept increasing when the number of prey increased. However, this assumption may not be realistic, especially under circumstances when the prey density is already high (e.g. near the carrying capacity of the system): at some point, there may be a physiological limit to how much a predator can eat. For example, digesting the biomass of one prey takes time and energy, which is not spent hunting for additional prey. In other words, there is a handling time associated with the consumption of each prey, which will also limit the maximum number of prey that a predator can consume within a certain timeframe.

*Figure 9.12: Passing out after a big meal: this pride of lions is in the process of digesting their recent kill. The time and energy spent digesting prey biomass is referred to as 'handling time'. Handling time was not considered in the models of Tutorial 5; this assignment will explore the consequences of including handling time for the emergent model dynamics, using the lion-buffalo system from Tutorial 5 as a starting point.*



In this case study, you will modify the predation term in the lion-buffalo model that was previously studied in class. Specifically, you will explain how the predation term needs to be rewritten (mathematically) to account for handling time, and subsequently analyze how this modification affects the behavior of the model system. Of particular interest is the way the emerging dynamics depend on the carrying capacity for buffalo of the study system. As done for the other population models studied in class, this analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits.

#### 10.3.4.2 Background for Case IV

The Lion-Buffalo model that was studied in Tutorial 5 can be viewed as one specific version of a more general predator-prey model:

$$\frac{dH}{dt} = rH - c_{HH}H^2 - f(H)P \quad (28)$$

$$\frac{dP}{dt} = ef(H)P - dP \quad (29)$$

Where  $f(H)$  is a function that describes the predation rate for one individual predator, also referred to as the *per capita predation rate*. In the Tutorial, we assumed for this function:

$$f(H) = c_{12}H \quad (30)$$

In the background for Case I, you can read how this function can be adjusted to include the handling time of prey in the predation function. This yields a new function  $f(H)$  that can be written as:

$$f(H) = \frac{c_{max}H}{b+H} \quad (31)$$

To see how this new function differs from the original function that was used in Tutorial 5, and the function used in Case I, it is very insightful to plot both these functions in a plot that varies  $H$  on the x-axis, and that shows the corresponding values of the three  $f(H)$  functions on the y-axis. Inserting equation (31) into equations (28) and (29) then yields the model that includes the handling time and the searching behavior at low densities. A possible starting point for this model is to use the following parameters:

$$r = 0.5 \quad b = 240$$

$$d = 0.04 \quad e = 0.2$$

$$c_{max} = 0.5$$

And see how the model behaves when one decreases the value of the the crowding parameter  $c_{HH}$  (e.g. from  $c_{HH} = 0.002$  to  $c_{HH} = 0.0005$ ). This can show you quite some different behaviors of the system, which are (given what the above parameter variation implies about the environment) actually quite counterintuitive. It will be an interesting case study to understand why these apparently paradoxical results emerge.



### 10.3.5 Case V: Human population dynamics and renewable resource consumption

What makes humans different from other species within the animal kingdom? This question can be approached from many angles, including a consumer-resource (or: predator-prey) perspective. From this perspective, particular attention has been paid to how human civilizations develop within areas with a finite amount of resources, such as island ecosystems.

One of the most debated examples of this kind is the history of Polynesian settlers on Rapa Nui, also known as Easter island. Close to a 1,000 moai (head statues) on the island suggest the presence of a large human population and society, but when European explorers arrived these societal structures and institutions were no longer present. Although widely disputed, one theory is that the large Easter island population suddenly collapsed due to the overexploitation of natural resources (in particular trees).

*Figure 9.13: What happened on Easter island remains a topic of fascination of historians, environmental scientists and social scientists alike. Although the archaeological evidence is casting doubt on the classical collapse narrative, the broader observation of rising and falling civilizations is supported for other historical societies as well. To what extent these societal dynamics can be understood from societal dependencies on natural resource availability can be studied with models like the ones studied in Tutorial 5, provided that some alterations are made to consider human behaviour.*



In this assignment, you will study under what conditions interactions between humans and a natural resource they depend on may lead to a sudden collapse of the human population. We assume that the natural resource can increase until the carrying capacity of the system is reached. In contrast to the predator-prey models studied in Tutorial 5, we assume that humans use of technology and capacity to organize will allow them to harvest the amount of resources needed, independent of the amount of resources present. We also assume that the carrying capacity of the human population is dependent on the amount of resources present (note that this is a coupling that we have not studied before). You can study how different scenarios of climate suitability (determining the growth rate of the resource) and human activity (determining the resource consumption rate) affect human population dynamics. As done for the other population models studied in class, this analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits.

### 10.3.2.2 Background for Case V

A starting point for this model can be to model a tree population, which, as we have seen in Tutorial 4, could be described by the logistic growth equation in the absence of human activity:

$$\frac{dR}{dt} = gR - \frac{g}{K}R^2 \quad (32)$$

Where  $g$  is the relative growth rate of the tree population, and  $K$  its carrying capacity as in the logistic growth model of Tutorial 3. Now, we consider that the humans on Easter Island are harvesting this tree resource. We could consider a similar harvesting term as we did in Tutorial 3, but in this case we can also consider the limited geographical settings on Easter Island, and assume that each human uses a certain amount of trees, and this use is considered essential (e.g. as fuel, or to build canoes, or to transport the moai). If we describe this per capita use rate with a parameter  $h$ , then the change in the tree population can be described by:

$$\frac{dR}{dt} = gR - \frac{g}{K}R^2 - hP \quad (33)$$

In which  $P$  is the human population size. For this human population size, we can also assume that it grows logistically. For the settings on Easter Island, we can then assume that the carrying capacity of the human population is dependent on the amount of trees that is (still) present on the island, as trees provide an essential resource. Specifically, we can introduce a parameter  $q$  which quantifies the number of humans that can be sustained by one unit of the tree population. Then, the human population dynamics can be described by:

$$\frac{dP}{dt} = rP - \frac{r}{qR}P^2 \quad (34)$$

For the settings of Easter Island, a realistic growth rate for the human population is  $r = 0.0044$ , and a realistic carrying capacity is  $K = 70000$ .

It is then of interest to study what type of human population dynamics can occur in this system, considering (combinations of) different social-ecological characteristics.

Vary the productivity of the environment from low (e.g.  $g = 0.5 * r$ ) to high (e.g.  $g = 4 * r$ ).

Vary the human harvest rate from low (e.g.  $h = r$ ) to high (e.g.  $h = 2r$ ).

Vary the human footprint from high (e.g.  $q = 0.15$ ) to low (e.g.  $q = 1.5$ ).

### 10.3.6 Case VI: Vegetation growth under water-limited conditions and desertification

Dryland ecosystems cover about 40% of the Earth's land surface, and provide a livelihood to more than 1 billion people. These livelihoods often depend directly on vegetation growth, through pastoral and agricultural activities. Due to the dry conditions, vegetation growth is most strongly limited by water availability. Importantly, water availability, specifically in the form of soil moisture needed for vegetation growth, not only depends on climatic conditions. It also depends on the effects of vegetation on the soil properties. We can use models to investigate the importance of these effects on dryland ecosystem functioning.

Specifically, we can model how precipitation, falling on the soil surface, will infiltrate into the soil. How much of the precipitation infiltrates, however, will depend on how much vegetation is there. The roots of vegetation may make the soil more loose, easing infiltration. In addition, we assume that vegetation growth depends on soil water availability, with vegetation approaching the maximum growth rates when soil water availability is high. We thus study a two-component model (consisting of the state variables vegetation and soil water availability).

*Figure 9.14: The experimental setup shown in this picture allows for measuring how the presence of vegetation affects infiltration of precipitation into the soil. On a sloping landscape, all the water that is running off the surface is collected at the collecting station in the corner. By measuring the amount of precipitation falling on the fenced area, the difference between collected water and precipitated water is the amount of water infiltrated into the soil. By performing this measurement for areas with different amount of vegetation cover, the relationship can be established. The assignment is to include this relationship in a soil-water vegetation model, and study how dryland ecosystems may respond to a change in rainfall regime.*



You can study how the system dynamics depend on climatic conditions (e.g. varying the precipitation rate), or on soil properties (e.g. how much water can infiltrate into an unvegetated soil). You can also study scenarios of climate change to see how the system responds to gradual changes in environmental conditions. As done for the other population models studied in class, this analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits.

### 10.3.6.2 Background for Case VI

We are considering a model with two state variables, water and vegetation. Water uptake is a flow from one state variable to the other, thus sharing some similarities with the predator-prey model that we considered in Tutorial 5. A general version of the water-vegetation model could then be written as:

$$\frac{dW}{dt} = \text{Infiltration} - \text{uptake} - \text{loss} = PPT * f_2(P) * - f_1(W) * P - r_w W \quad (35)$$

$$\frac{dP}{dt} = \text{Growth} - (\text{mortality} + \text{respiration}) = e * f_2(W) * P - (d + b) * P \quad (36)$$

Where PPT is precipitation,  $r_w$  is the relative loss rate of water from the system,  $d$  is the plant's relative mortality rate and  $b$  is the plant's relative respiration rate, and  $e$  the efficiency of turning water into vegetation biomass. We see that the dependencies between water and vegetation are described by the functions  $f_1(P)$  and  $f_2(W)$ . Specifically,  $f_1(P)$  describes how plants alter the structure of the soil, so that water can infiltrate more rapidly into the soil. This function could be described by:

$$f_2(P) = \frac{P + k_2 W_0}{P + k_2} \quad (37)$$

In which  $W_0$  is the amount of water that would infiltrate into the soil if there are no plants, and  $k_2$  is the plant density where the system reaches half of the maximum infiltration rate. In addition, the function  $f_1(W)$  describes the process of water uptake:

$$f_1(W) = c_{max} \frac{W}{W + k_1}$$

In which  $k_1$  is the water availability at which the plant reach half the maximum uptake rate,  $c_{max}$ . For this system, realistic parameters can be:  $e=10$ ,  $c_{max}=0.5$ ,  $k_1=3$ ,  $d=0.1$ .

It is then of interest to study how different plant characteristics, soil properties and environmental conditions may affect the system dynamics, for example, it is interesting to study:

Vary the respiration rates of plants from low (e.g.  $b = 0.15$ ) to high (e.g.  $b = 0.35$ ).

Vary the infiltration rate of bare soil from low (e.g.  $W_0 = 0.2$ ) to high (e.g.  $W_0 = 0.9$ ).

The influence of plant growth on water infiltration from high (e.g.  $k_2 = 5$ ) to low (e.g.  $k_2 = 25$ ).

### 10.3.7 Case VII: Vegetation growth in alpine ecosystems

Alpine ecosystems form unique environments, in which vegetation survives under relatively harsh conditions. The vegetation adapted to these conditions is distinctly different from lowland ecosystem vegetation, highlighting the biodiversity conservation value of alpine systems. One particular characteristic of alpine environments is the slow rate of soil formation, and hence nutrient accumulation in these systems. The relatively low availability of nutrient is a limiting factor for plant growth. Importantly, soil nutrient availability, not only depends on the parent material (i.e. bedrock) and atmospheric deposition rates, but also on the presence of vegetation itself. The roots of vegetation play an important role in stabilizing soils in alpine ecosystems, thereby limiting soil erosion rates and the accompanying loss of nutrients from the system. We can use models to investigate the importance of this effect on alpine ecosystem functioning.

*Figure 9.15: Example of a Swiss alpine ecosystem where an area with low vegetation cover experienced erosion that was associated with the spring snowmelt. Loss of soil and soil nutrients may subsequently hamper vegetation regrowth. This illustrates how the vegetation in this type of ecosystems has an important role in maintaining the environmental conditions that are conducive to vegetation persistence and growth. The assignment is to study this role in a soil nutrient-vegetation model, and study how alpine ecosystems may respond to changes in climatic conditions (e.g. increased susceptibility to erosion due to faster snowmelts or increased frequency of heavy precipitation events).*



Specifically, we can model how precipitation, falling on the soil surface, will infiltrate into the soil. How much of the precipitation infiltrates, however, will depend on how much vegetation is present. The roots of vegetation may make the soil looser, easing infiltration. In addition, we assume that vegetation growth depends on soil water availability, with vegetation approaching the maximum growth rates when soil water availability is high. We thus study a two-component model (consisting of the state variables vegetation and soil water availability).

You can study how the system dynamics depend on climatic conditions (e.g. varying the precipitation rate), or on soil properties (e.g. how much water can infiltrate into an unvegetated soil). You can also study scenarios of climate change to see how the system responds to gradual changes in environmental conditions. As done for the other population models studied in class, this analysis includes both numerical analyses through model simulations and analytical analysis using state space portraits.

### 10.3.6.2 Background for Case VI

We are considering a model with two state variables, nutrients and vegetation. Nutrient uptake is a flow from one state variable to the other, thus sharing some similarities with the predator-prey model that we considered in Tutorial 5. A general version of the water-vegetation model could then be written as:

$$\frac{dN}{dt} = \text{Input} - \text{uptake} - \text{loss} = N_{in} - f_1(N) * P - f_2(P)N \quad (35)$$

$$\frac{dP}{dt} = \text{Growth} - (\text{mortality} + \text{respiration}) = e * f_1(N) * P - (d + b) * P \quad (36)$$

Where  $N_{in}$  is the atmospheric input of nitrogen (a constant),  $d$  is the plant's relative mortality rate and  $b$  is the plant's relative respiration rate, and  $e$  the efficiency of using nutrients to produce vegetation biomass. We see that the dependencies between nutrients and vegetation are described by the functions  $f_1(N)$  and  $f_2(P)$ . Specifically,  $f_1(N)$  describes how plant growth (and uptake) depend on nutrient availability, so that plants grow more rapidly under higher nutrient availability:

$$f_1(N) = c_{max} \frac{N}{N + k_1} \quad (37)$$

In which  $c_{max}$  is the maximum growth rate, and  $k_1$  the nutrient availability where the plant reach half their maximum. In addition, the function  $f_2(P)$  describes how vegetation may reduce the amount of soil that is lost through erosion:

$$f_2(P) = r_{max} \frac{k_2}{k_2 + P}$$

In which  $k_1$  is the plant density at which half the maximum erosion rate,  $r_{max}$  occurs. For this system, realistic parameters can be:  $e=10$ ,  $c_{max}=0.5$ ,  $k_1=3$ ,  $d=0.1$ .

It is then of interest to study how different plant characteristics, soil properties and environmental conditions may affect the system dynamics, for example, it is interesting to study:

Vary the sensitivity of the soil to erosion from low (e.g.  $r_{max} = 0.2$ ) to high (e.g.  $r_{max} = 0.5$ ).

Vary the impact of the vegetation on soil erosion from low (e.g.  $k_2 = 400$ ) to high (e.g.  $k_2 = 25$ ).

Vary the respiration rate of plants from low (e.g.  $b = 0.05$ ) to high (e.g.  $b = 0.15$ ).