

Qualitative models of population dynamics

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Abstract

Conceptual models are important means for ecologists towards ecological theory development. Qualitative reasoning can be used to represent and simulate conceptual models. Such models represent knowledge about structure, causality, active processes, and the qualitatively distinct behaviours of the system. This thesis discusses the development and evaluation of a qualitative model in the field of population ecology, and includes the following aspects. A review of the literature identifying the important principles underlying populations and communities in nature. A design and implementation of a qualitative model formalising these principles following the structured approach to modelling developed in the NaturNet-Redime project. A model test and model evaluation by (1) running simulations with the model in different scenarios, (2) comparing the model to a competing approach referred to as the R-star model, and (3) an expert review using two domain experts.

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1. Introduction

1.1 Introduction to the problem

The field of qualitative reasoning and modelling concerns itself with creating models that represent real world systems and their behaviour. Qualitative reasoning (QR) relies on knowledge about causality and processes, gained from experts of a particular domain. The qualitative representation of this knowledge in a model reduces complexity and makes it possible to predict and explain the behaviour of the system in a systematic and formal way.

An interesting field of application is ecology, which researches and theorizes about complex systems in nature. Qualitative reasoning and modelling can help ecologists to gain insight and explanations about the behaviour of the systems they study. Without requiring extensive quantitative data, qualitative models can be created that simulate the behaviour of the chosen real world system while also explaining why this behaviour occurs. These are features that are more difficult to achieve with traditional modelling methods. (Salles et al., 2003)

The goal of this thesis is to gain insight into the dynamics of population and community ecology and how these principles can be modelled qualitatively. Adhering to the software engineering principle of reusability, a model will be created that captures the basic principles underlying population dynamics and which can be re-used in specific scenarios. To reach this goal, the following research question will be addressed:

Which basic principles of population ecology can be identified and implemented into a compact and reusable qualitative model, which can be used to give insight in the complex dynamics underlying the theory?

1.2 Method and evaluation of the results

The goal of this project is to create one or several qualitative models that capture the principles underlying population dynamics. Several model fragments will be created which will be reusable when constructing these models. These model fragments reflect the main principles of food web theory and could be a starting point for the creation of a complete set of such re-usable fragments in future research. The research in this thesis first reviews ecology literature to gain understanding of the dynamics of population and community ecology. From this study insight into the main principles of the theory will be derived. Also, an overview and explanation of qualitative reasoning theory and the modelling primitives is given.

Next, the modelling tasks are executed by following the methodology developed in the NaturNet-Redime project (Bredeweg et al., 2005). The evaluation of these models and the simulation results is done in three steps. The first evaluation step is to compare the simulation results of the models to the descriptions of the system behaviour in the literature. When comparing this expected behaviour to the simulated behaviour it becomes clear whether or not the model captures the real world system adequately. The second evaluation step is a comparison to a competing approach referred to as the R-star model (Nuttall et al., 2006). The third evaluation step concerns expert reviews. Two ecology experts are asked to analyse the model and give their opinion, following a structured interview. To determine whether the developed model is in principle reusable, it is used in an extended model including multiple populations. The simulation results of this complex model are compared to the predictions derived from the theory.

1.3 Organization of the report

In chapter 2 an explanation of qualitative reasoning and modelling is given. This section is then continued with a description of the modelling primitives used in the Garp3 software package and an explanation of how this software works. Also, a simple example of a model implemented in Garp3 is given to create familiarity with the sequence of modelling steps and the representation of modelling primitives in the

software. In chapter 3 an extensive review of relevant ecology theory is given following a process centred view. This chapter provides the focus concerning what knowledge must be dealt with in the modelling task. In chapter 4 the modelling choices and implications are elaborated upon and an overview of the created model and the simulation results are given. In chapter 5 the comparison is made to the R-star model. An overview of the most important features of the R-star model is given and compared to the model presented in chapter 4. In chapter 6 the reusability aspect of the model developed in chapter 4 is addressed by constructing a model that includes a predator prey interaction between two populations. An overview of the model fragments, scenarios and the simulation results is given and explained. In chapter 7, the results of consulting two domain experts are given. In chapter 8, the main results will be summarized and discussed. This chapter ends with suggestions for future research.

2 Qualitative Reasoning Theory

2.1 Introduction

One of the fundamental aspects of Artificial Intelligence (AI) focuses on problem solving tasks and reasoning about the physical world (Russel & Norvig, 1995). A goal of AI research is to understand and reproduce the way humans go about their tasks in this physical world, continuously reasoning and solving problems they encounter.

Qualitative reasoning is motivated by the observation that human reasoning and problem solving does not need to be described by mathematical models. Without applying or even possessing knowledge of formal theories to reason about the world in a numerical and systematic way, humans are able to interact with and reason about their environment. There is some basic conceptual knowledge humans have about how the physical world around them reacts to changes. Qualitative reasoning research aims to understand and to be able to formally represent this conceptual knowledge about the physical world.

Simulations are regarded as a useful tool to create more insight into complex real world systems and to support making decisions about them. Simulations require models of the system in order to work and one of the subjects of research in qualitative reasoning is creating qualitative models that represent complex real world systems. Qualitative physics reduce complexity and makes it possible to create models of systems without losing important information about their behaviour. Creating these models is difficult and requires the identification of relevant objects and interactions, their important properties and quantities, but also a reduction of complexity by determining what is relevant and what is not. A formal language to describe these models has to be developed and understood by the model builder. Expressing the system into this language makes it possible to draw conclusions about possible behaviours of the system (Bredeweg & Struss, 2003).

A formal language to express qualitative models is found in ‘Qualitative Process Theory’ developed in 1984 (Forbus, 1984). The theory of confluences, qualitative differential equations that can be used for modelling behaviour of components in larger systems, was developed in the same year (De Kleer & Brown, 1984). Further research led to the notion of compositional modelling, which gives a theoretical framework to create a model out of several model fragments and a scenario (Falkenhainer & Forbus, 1991).

GARP integrates these previous approaches and provides its own formal vocabulary of modelling primitives, which can be used to express real world systems into models that can be simulated (Bredeweg, 1992). Since its initial development it has undergone significant changes and is currently transformed into a complete software package that enables a model builder to build models, run simulations on the constructed models and explore the derived behaviour it shows. This software package is called Garp3. More information about Garp3 and its development can be found on <http://hcs.science.uva.nl/QRM/>.

2.2 Qualitative modelling and simulation

Figure 2.1 shows an overview of all aspects involved in the process of qualitative simulation. Four parts are distinguished in the process, the library of model fragments, the collection of scenarios that include initial values and assumptions, the reasoning engine and the result of the reasoning process, which is a state-graph of qualitative states.

To create qualitative models, a formal language of modelling primitives must be used and understood. These modelling primitives can be used as building blocks to create structures that represent parts of the model. Together these structures, called model fragments, make up the library that contains all information about the possible changes within the system. After the model fragments are made, the scenario that includes the initial values and assumptions about the initial situation of the simulation has to be created. Scenarios can be created the same way in which model fragments are created, with the building blocks provided by the modelling environment.

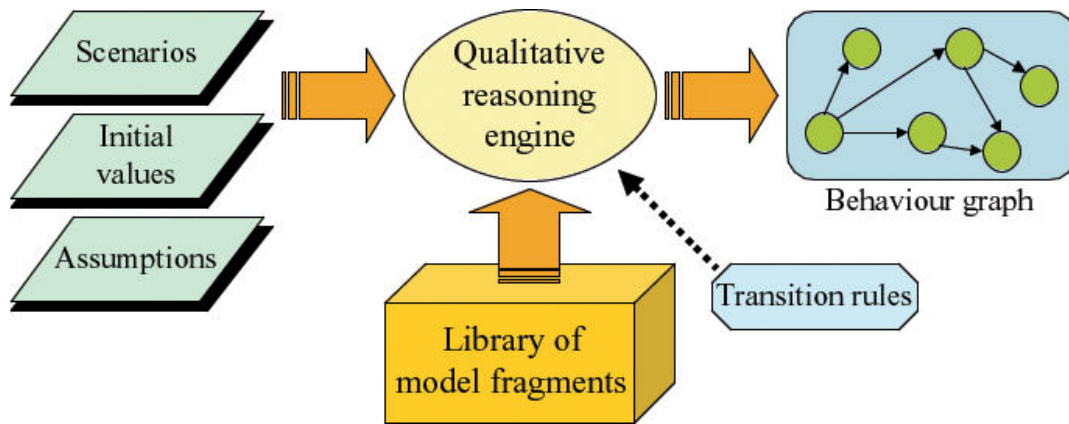


Figure 2.1: The structure of qualitative simulations in GARP.

The reasoning engine is part of Garp3 and consists of an extensive set of transition rules. The engine starts with reading the scenario, which contains information about the initial state of the values within the system and assumptions that are made. Then it searches the model fragment library for references on what states could possibly follow from the scenario. The qualitative reasoning engine then uses a set of transition rules to determine how and what transitions can manifest between states. This leads to a state-graph of successive qualitative states. Each qualitative state represents a unique possible state of the system. Together a path of successive states represents a possible behaviour of the system.

2.2.1 Incorrect models and simulations

When performing a qualitative modelling task, modelling errors may occur. Errors can be made when constructing the model fragment library and while constructing the scenario. Sometimes errors are made when choosing the modelling primitives to construct the model fragment library, which can result in incorrect behaviour when inspecting the state-graph. Also, incorrect use of the modelling primitives can result in conflicting model fragments that may prevent the reasoning engine from finding any possible states when considering the scenario and the model fragment library. When the scenario is faulty it may miss some essential ingredient or cause conflicts with the facts found in the model fragment library, which can cause incorrect behavioural paths or no states at all when simulating. In section 2.3.6, some tools available in Garp3 are explained and shown, which can be used to inspect the simulation results for correctness.

2.2.2 Model building methodology

The NaturNet-Redime project has developed a framework that provides a structured approach to building qualitative models (Bredeweg et al., 2005). This framework was developed to facilitate comparison of case studies results within the NaturNet-Redime project. It specifies 6 sequential phases for the development of a qualitative model:

- Orientation and initial specification – This step establishes what is going to be captured in the model and why a qualitative model of these phenomena is useful. It should also specify what the goal is and who the end users are. In this step, concept maps can be useful and their use is recommended to gain insight into the structure of related concepts in the domain.
- System selection and structural model – This step serves to identify the parts and the structure of the selected system. Also, decisions about including and excluding parts of the system have to be motivated and made explicit as assumptions about the system structure.
- Global behaviour – The result of this step is a description of the behaviour that has to be captured in a causal model. Several aspects of the behaviour have to be identified: the most relevant processes, external influences and deliberate actions. Also, the scenarios and the expected behaviour should be specified. In this step, the assumptions also need to be represented explicitly.
- Detailed system structure and behaviour – This step is essentially a refinement of the results obtained in the previous steps. The structural details, scenarios and assumptions are defined using

the modelling vocabulary of the target engine. Finally, a plan is made which provides directions for the implementation phase about the conditions for model fragments to become active and the consequences they introduce in the model.

- **Implementation** – This is the step in which the actual implementation into Garp3 occurs. When implementing the results from the previous steps, usually some debugging needs to be done and changes need to be made, to have the simulations produce the expected behaviour.

The framework also provides guidelines for the documentation of the model to further optimise the communication about models and modelling decisions.

For the work presented in this thesis the above described methodology is used, but the thesis itself does not follow the guidelines for documentation and the vocabulary standards. This is because it does not focus on comparison but on presenting the results, which can be used to answer the research question, which does not require such detail.

2.3 Modelling primitives

In this project the latest version of the Garp3 software package is used. A full list of all the available primitives in the GARP reasoning engine is available in Appendix B. To describe and explain frequently used primitives in the modelling task, a running example is used as a guideline in this section.

2.3.1 Example: the U-tube system

A u-tube is a system that consists out of two or more connected containers filled with the same fluid. The connection between the containers is a pipe through which the fluid can flow from one container to the other. Fluids travel through the pipe under influence of difference in fluid pressure between the containers. The level of the fluid in the container causes fluid pressure in a container. This means that difference of pressure between containers is caused by a difference in level of the fluid in each container. When the fluid travels through the pipe it will always travel from the container with higher pressure towards the container with lower pressure, until the pressures in both containers are equal. The fluid levels of both containers will then also be equal.

2.3.2 Building blocks

To begin with, each qualitative model has some building blocks that define the static structure of the system that is represented. These building blocks are entities, configurations, quantities and assumptions.

Entities

Entities represent the physical objects that make up the system, such as the environment or a population. In Figure 2.2 the entity hierarchy of the u-tube system is shown.

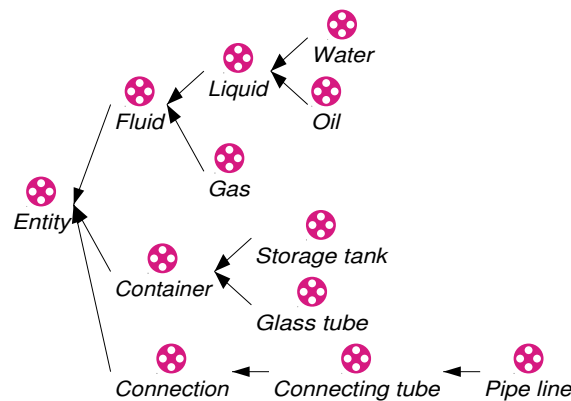


Figure 2.2: The entity hierarchy of the U-tube system.

In the example several entities can be distinguished, such as container, pipe and fluid. Entities are ordered into a subtype hierarchy so that generic parent types can be further specified into the actual system parts that exist in the real world. Container can be further specified into storage tank, pipe into connecting tube and fluid into gas and liquid, and liquid into oil to model a specific u-tube system that includes oil tanks.

Configurations

Besides the physical objects of the system, the structural relations between these physical objects must be defined. These relations are called configurations in Garp3 and define how physical objects relate to each other. The configurations of the u-tube system are shown in Figure 2.3. It can be said that the container in the u-tube system contains the fluid, so the configuration between container and fluid is *contains*. Also, the pipe connects both containers to each other and is connected to each container. That means there must be a configuration connecting container A to the pipe and another configuration connecting the pipe to container B. These configurations can both be from the same type: *connects*.

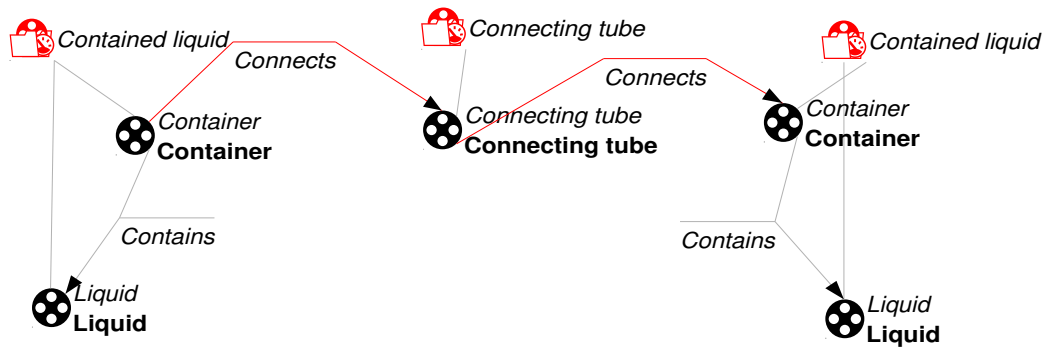


Figure 2.3: The entities and the configurations in the U-tube model. The container on the left is considered to be container A, the container on the right is container B.

Quantities

After defining the physical structure of the system, those aspects that describe the changeable properties of the system are added. The representations of these aspects in the u-tube model are shown in Figure 2.4. Quantities are those aspects of entities that can change under the influence of other aspects of the system. In the introduction of the u-tube system several variables were mentioned, such as pressure, level, amount, the ability of the pipe to transport fluid and the direction of the fluid flow. It is important to attach the right quantities to the corresponding entities for the end result to be conceptually correct.

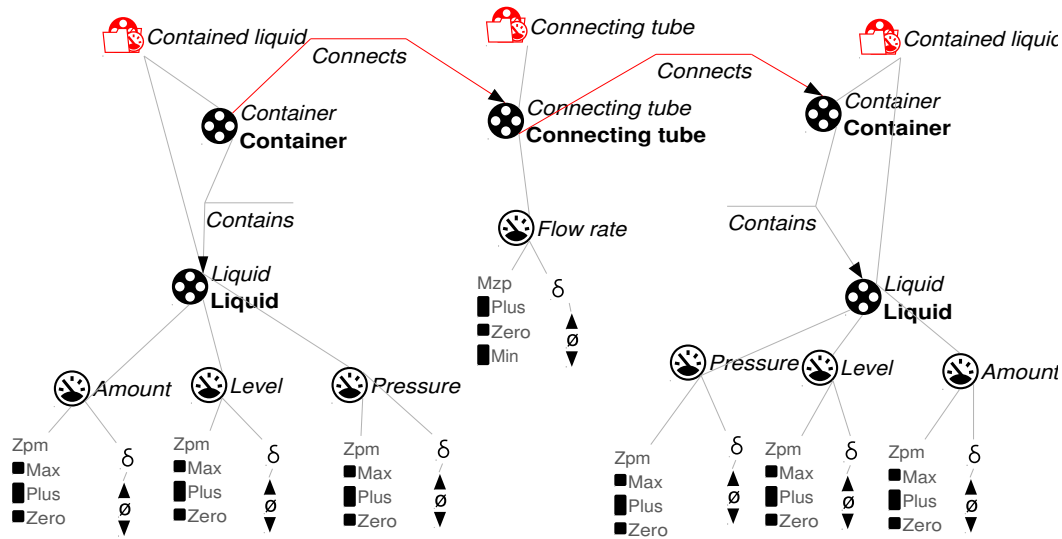


Figure 2.4: The quantities in the U-tube model.

In the u-tube three important entities are defined, container, fluid and pipe. Container has no important changeable properties in this system because it is unlikely that the container will change in shape or size while fluid flows in or out of it. The properties Pressure, Level and Amount must be attached to fluid for it is the fluid inside of the container that changes in amount, level and pressure when it flows into or out of a container. The pipe can transport the fluid from one container to the other, but it can be transported both ways, which depends on the state of the system. The quantity that determines whether there is a flow of fluid in the pipe and which direction this flow takes, is called Fluid_flow.

Quantity spaces

Quantities have quantity spaces that define the range of possible values for quantities. All values in the quantity space are qualitative values, which means they can be points or intervals. Points define important landmarks of the properties of the system while intervals define the range of values between two points. Zero is a point, where Small as an interval can be a range between two points, Zero and Medium. Most quantity spaces include the value Zero as an important landmark. Pressure of a fluid can be zero, but it cannot be less than zero, so Zero will define the lowest point in the quantity space. The value of the pressure can also become more than Zero, which will be defined as Plus, because it is a positive value. There also is a point of maximum pressure, because pressure cannot become infinite, which will be described as Max. The quantity space for Pressure can be {Zero(point), Plus(interval), Max(point)}. Level and Amount have the same quantity spaces as Pressure. The quantity space of the Fluid_flow in the pipe is different, because the fluid can flow both ways. The direction of the flow is what matters and can also be captured in a quantity space {Min(interval), Zero(point), Plus(interval)}. Plus and Min describe the possible directions of the flow and Zero means there is no flow.

Derivatives

Another important aspect of a quantity is the derivative. The derivative describes the changes of the quantity and always has quantity space {Min, Zero, Plus}. Min means the quantity is decreasing in magnitude, Zero means it is stable and Plus means the quantity magnitude is increasing.

Quantity values

To describe the current value of a quantity the notion of quantity value is used. This value consists of two parts, the magnitude and the derivative. The magnitude of the quantity is the value of the quantity and the derivative describes whether the quantity is decreasing, stable or increasing in magnitude.

Assumptions

Other useful building blocks of qualitative model fragments are assumptions. These can be used to define certain properties of a system as conditions. In a real u-tube system, containers can be of various sizes. Differences in size between containers could make one of the containers overflow when the fluid is transported there. An assumption that the containers are cannot overflow, could be added to the model. Assumptions can be added as structure elements to the model to make the use of these modelling choices explicit to the reasoning engine.

To simplify the model discussed here, it does not include explicit assumptions. However, the ecology part of this thesis does require assumptions, and the explanation of their implementation will be elaborated upon in chapter 4.

2.3.3 Dependencies

Dependencies are those elements of the model that represent behavioural constraints. They can change quantity values directly or indirectly and connect quantities through causal relations. Figure 2.5 shows the dependencies used when modelling the liquid in the container.

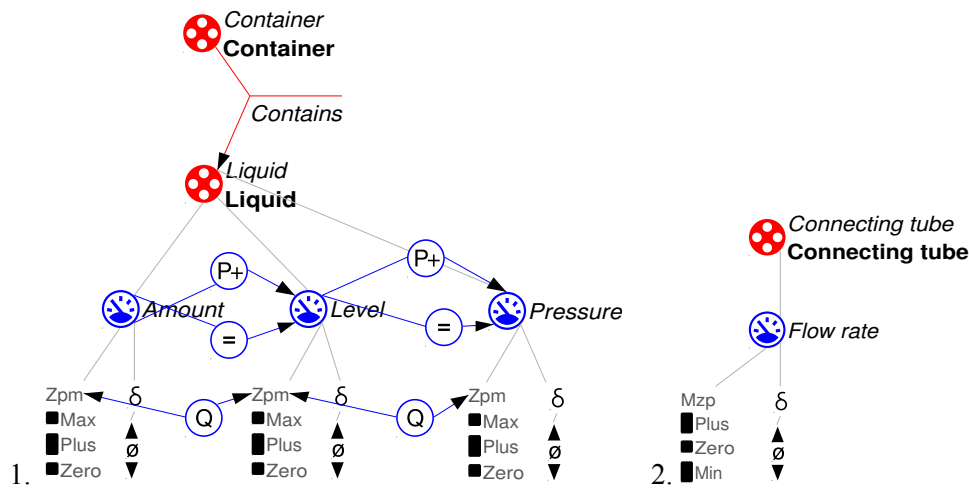


Figure 2.5: 1. The complete *Contained liquid* model fragment.
2. The *Connecting tube* model fragment.

Proportionalities

The entity fluid has quantities Pressure, Level and Amount to describe the different properties of the fluid. These three quantities react in the same way to changes of the fluid. Changes start at an increase or decrease of the fluid Amount and end by leading to the increase or decrease of the Pressure.

To model this, proportionalities are used. Similar to configurations, proportionalities are directed from one model element to another with the only difference that the initial and target elements are both quantities. Proportionalities model the indirect effects of processes. They propagate the effects of a process and set the derivative rather than the magnitude of the target quantity. Proportionalities can also be positive or negative. $P+(B, A)$ means that changes in A, in a particular direction cause B to change in the same direction. $P-(B, A)$ means that changes in A, in a particular direction, cause B to change in the opposite direction. Changes in Amount will cause changes in the same direction in Level, and changes in Level will cause changes in the same direction in Pressure. Positive proportionalities need to be defined from Amount to Level and from Level to Pressure. The proportionalities are represented by the directed P+ arrows in Figure 2.5.

Correspondences

To describe the changes in Amount, Level and Pressure are exactly the same and occur simultaneously, correspondences are needed. Correspondences are means to reduce ambiguity by indicating that values in quantity spaces change in the same way and thus have the same qualitative values. Correspondences can

be directed or undirected, meaning that respectively the target value changes when the source value changes or that when either value changes the corresponding value also changes. To indicate Amount, Level and Pressure correspond, undirected correspondences between the quantity spaces are used. The undirected correspondences are represented by the arrows with the Q symbol in Figure 2.5.

Inequalities

Quantities with the same quantity space, which are influenced in the same way, are not necessarily equal in quantity value. Medium in one quantity space can be greater than Medium in another quantity space. The outcome of many processes depends on the equality relations between quantities, so it is desirable to express whether or not quantities are comparable.

Inequalities are ordinal relations expressing equalities and inequalities between quantity values in the system. Inequalities can be $<$, \leq , $=$, \geq , and $>$. There are several possible ways to use inequalities, because of the possibility to connect them to magnitudes, points of magnitudes, derivatives, zero point of a derivate and Plus or Min relations. Inequalities are always created between points, as it is not possible to define them for intervals. To indicate that amount, level and pressure are in fact equal to each other, equality statements are introduced from amount to level and from level to pressure. The equality relations are represented by the directed arrows with the equality symbol ($=$) in Figure 2.5.

Plus or Min relations

To model the fluid flow through the pipe yet another dependency is needed. The fluid will only flow when there is a difference between the pressures of the fluids on both sides of the pipe. This difference must be calculated to determine if there is a flow and what the direction of the flow is. To this end, the Plus or Min relation is used. With Plus or Min relations differences and sums of magnitudes, points in the quantity space of a magnitude and derivatives can be calculated. Plus or Min relations can be the target or the source of inequality relations. They can also be connected to other plus/min relations or be connected by several inequalities. To determine the difference between two pressures, a Min relation is added between the two pressure quantities, which belong to the fluids in the two connected containers, as shown in Figure 2.6. The result is then assigned to the flow quantity of the pipe with an equality relation. This results in Zero flow when both pressures are equal and Min or Plus when the pressures are not equal.

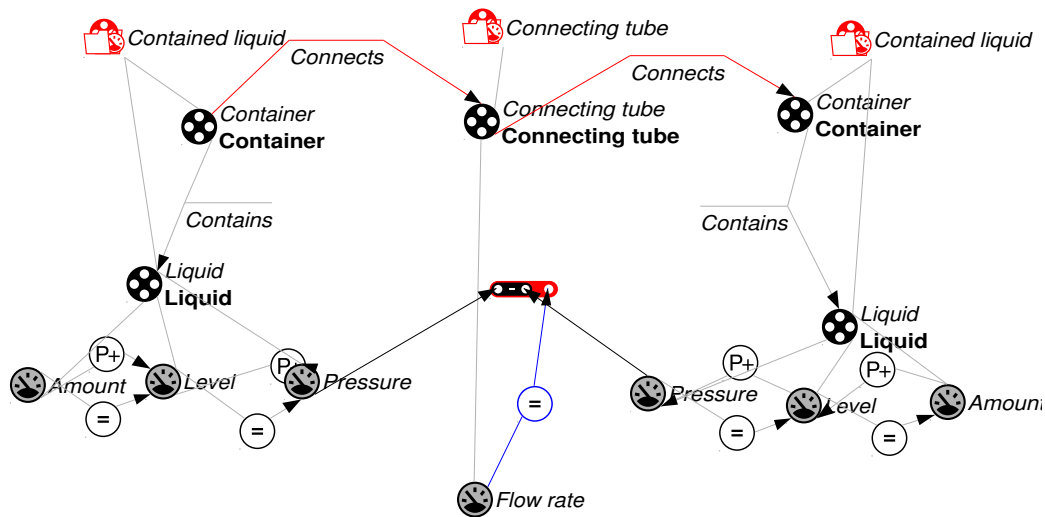


Figure 2.6: The min relation that calculates the magnitude of flow rate.

Influences

The contained fluid and the fluid flow are both modelled, but there are still two important aspects of the system that need to be included in the model: how the flow affects the fluid amounts in both containers and how the fluid pressures affect the changing of the flow.

As mentioned earlier, the flow causes the fluid amount to decrease in one container and to increase in the other. To model this, yet another type of dependency is needed. Processes are modelled by influences, directed relationships between quantities. Influences can be positive or negative. The source magnitude and the type of influence determine whether the derivative of the target quantity increases or decreases. $I+(B, A)$ means that there is a flow A that causes B to increase when A has a positive magnitude and decrease when A has negative magnitude. $I-(B, A)$ means that there is a flow A that causes B to decrease when A has a positive magnitude and increase when A has a negative magnitude.

When the fluid pressure in container A is bigger than the fluid pressure in container B, the flow of fluid between container A and B will be found positive or Plus by calculating the difference. This means the fluid flows from A to B, causing a decrease in the fluid amount of container A and an increase in the fluid amount of container B. To model this there needs to be a negative influence from the Fluid_flow to the Amount in container A and a positive influence from the Fluid_flow to the Amount in container B. The other option is that the fluid pressure in container A is smaller than the fluid pressure in container B. The flow of fluid from container A to container B will be found negative or Min by calculating the difference and thus the fluid flows from B to A. This causes an increase in the fluid amount of container A and a decrease in the fluid amount of container B. By creating the same negative influence from the Fluid_flow to the Amount of container A and a positive influence from the fluid flow to the fluid amount in container B. When the Fluid_flow is Zero, the influences will also be zero, letting both fluid amounts to stay the same. The influences are represented in Garp3 as directed arrows with an $I+$ or $I-$ sign, as shown in Figure 2.7.

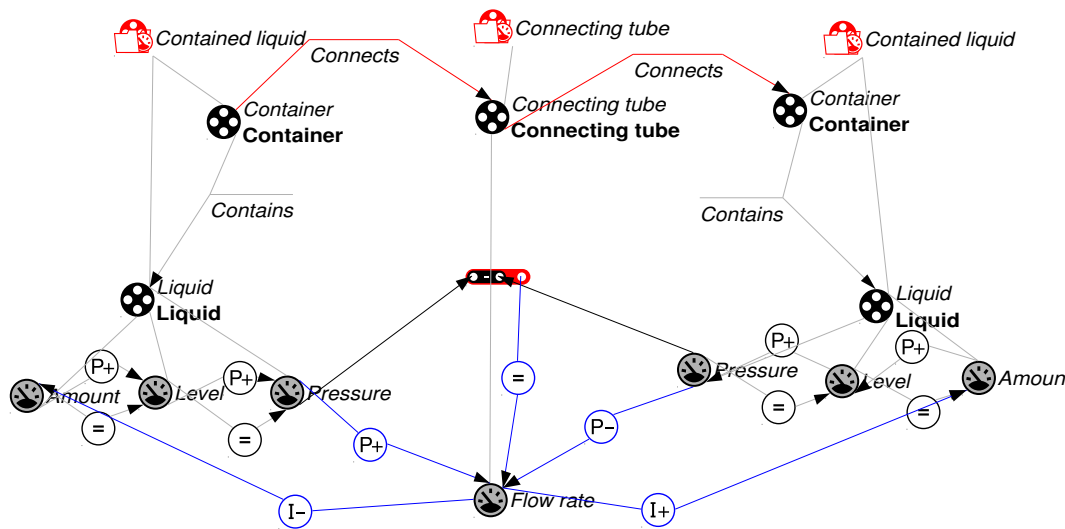


Figure 2.7: The complete *U-tube* model fragment.

Finishing the model

To model how the fluid pressures affect the changes of the flow, proportionalities are needed again. When the amounts change under influence of the flow, through the proportionalities, correspondences and inequalities, the levels and pressures of the fluids change in the same way. This also causes the inequality relation between the two fluid pressures to change. When calculating the difference again for the new situation, the magnitude of the flow may also change. But the Min relation in the model only assigns a magnitude and the derivative of the flow must also be calculated. The derivative describes the changes of a quantity and without it, it is not possible to determine when and if the quantity changes. Proportionalities are added between each fluid pressure and the fluid flow in the pipe to determine the value of the derivative of the fluid flow. Proportionalities and also influences from quantities have relative strengths, calculated by the inequality relations between both source quantities. When two proportionalities are targeting one quantity they are added and the outcome is determined by the sign and the value of both dependencies.

When looking at container A and B, the flow will be greatest when the difference between the fluid pressures is greatest. The flow will decrease in strength when the difference becomes smaller. When pressure in A decreases, because the fluid flow goes from A to B, the pressure in B simultaneously increases, and fluid flow should decrease towards *Zero*. This means that a decrease in fluid pressure A and an increase in pressure B both cause a decrease in the fluid flow. This is modelled by a negative proportionality from fluid pressure A to fluid flow and a positive proportionality from fluid pressure B to fluid flow. The other way around, when there is a flow from B to A, the flow will also be greatest when the difference between both fluid pressures is greatest, but now the flow is mirrored and fluid flow will be negative. When fluid pressure A increases and fluid pressure B decreases, fluid flow will slowly go from *Min* towards *Zero*, and thus its derivative is positive, although conceptually the strength of the flow is decreasing. This is also modelled by a negative proportionality from fluid pressure A to fluid flow and a positive proportionality from fluid pressure B to fluid flow. When the fluid pressures are equal to each other, the fluid flow will stabilize. The final Figure including all the aspects of the u-tube system is shown in Figure 2.7.

2.3.4 Model fragments

A model of a system consists of several parts working together. In qualitative modelling, these parts, created out of building blocks and dependencies by the model builder, are called model fragments. Model fragments are rule based and every ingredient added to the fragment is either a condition or a consequence. Conditions are those model ingredients that have to be true in order for the model fragment to be added to the scenario by the simulator and the consequences to be executed as facts about the system's behaviour. Consequences are those ingredients of a model that are added to the simulation structure when the conditions of the model fragment are met. The rule based nature of the model fragments follows the format: if the conditions are met, then the consequences are added to the current state of the system.

In Garp3, conditional model elements are red and consequence model elements are blue. This can be illustrated when looking at Figure 2.5 again. The liquid, the container and the connecting tube are added as conditions and the quantities and dependencies as consequences. This is important for the creation of scenarios, which is described in the next section.

There are several types of model fragments. Static model fragments are those structures of model ingredients that do not contain influences. Their purpose is to describe the basic structure of the system including the proportionalities that exist between quantities. In the u-tube system there are two static model fragments, *the contained liquid* and *the connecting tube*, both shown in Figure 2.5.

The other type of model fragment that is used in the u-tube system is a process fragment. Process fragments are those structures that do contain direct influences. The purpose of these model fragments is to describe the processes that take place in the system. There is only one process model fragment in the u-tube system, which is the complete u-tube model fragment shown in Figure 2.7.

2.3.5 Scenarios

A scenario is a description of a specific situation stating the conditions that are true at the beginning of the simulation. Ingredients added in a scenario must be matched by model fragments. Consequences will be added to the system structure when the simulator can match the conditions of one or several model fragments to those stated in the scenario. These consequences can start processes, which in their turn can lead to multiple connected states from which behaviour can be derived. The scenario for the u-tube model is shown in Figure 2.8. It implements the basic structure of the system, which is also shown in Figure 2.3.

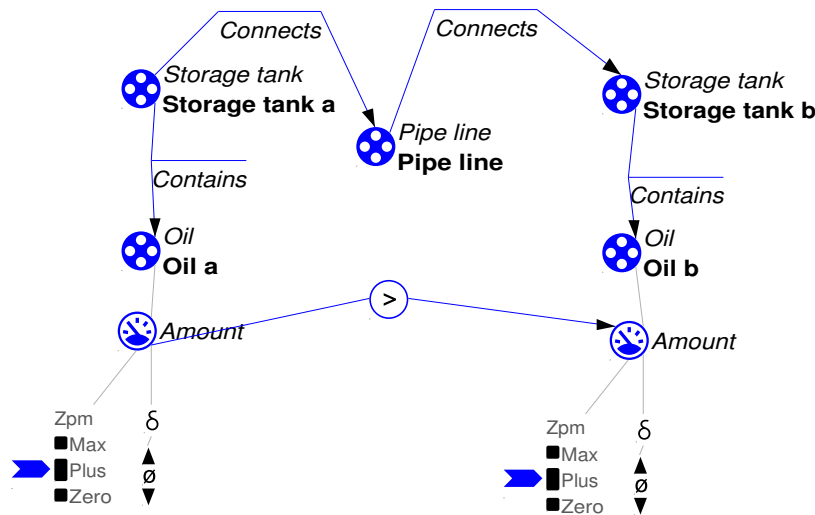


Figure 2.8: The U-tube scenario.

The two oil amount quantities are added only to define initial values for the reasoning engine to start the simulation with. The inequality statement is added between both quantities to define the initial condition that there is more oil in storage tank A than in storage tank B.

2.3.6 Simulation results

Simulations of qualitative models in Garp3, result into a representation of possible behaviours as graphs of successive states. This sequence of states describes the behaviour of the system that is captured in the model. States contain information about the system in a particular situation, such as the scenario, but derived with the transition rules of the reasoning engine and the model fragments from the library, which become active when certain conditions are met. The transitions between states determine how states follow from and out of each other. Together a directed path of successive states represents a possible behaviour of the system.

Ambiguity

Qualitative reasoning reduces complexity considerably, making simulations of complex systems fast and keeping them relatively simple to interpret. But, because of the qualitative nature of the modelling, ambiguity can occur, which reduces the correctness of the simulation results because the interpretation of the behaviour will be ambiguous as well. A good model reduces both complexity and ambiguity.

More states and many connections between the states mean that there is more complexity and ambiguity in the behaviour, signalling there are many possible transitions from the initial state of the scenario. Without some restrictive information the reasoning engine tries all possibilities from one transition to another. When quantity spaces get larger the amount of possibilities increases. When there is not sufficient information about the outcome of an influence on a quantity, this quantity can increase within an interval, stabilize, decrease, or make the transition to a point value while stabilizing or changing still. The amount of possibilities increases exponentially with each influence or proportionality between two quantities, resulting into state-graphs that include many connections and many more states, thus adding to the ambiguity.

Smaller state-graphs make it easier to see modelling errors and bugs and to interpret the behaviour of the simulation. However a large and not very insightful state-graph does not mean that the model or scenario is faulty, but it may be desirable to reduce ambiguity anyway to make it easier to evaluate the simulation and interpret the behaviour. Sometimes reducing ambiguity required making concessions on the conceptual correctness of the model, by setting boundaries and making assumptions on aspects of the model that are not the focus of the modelling task. Making the right assumptions to reduce ambiguity can influence the correctness of the outcome of the simulation considerably and thus requires extensive knowledge of the domain.

Simulation of the U-tube

Before the simulation starts in Garp3, the reasoning engine predicts one or several initial states that can follow from the scenario. The initial states are yellow like state 1 in Figure 2.9. From this initial state several paths of successive states follow, that together form the state-graph. The state-graph of the u-tube simulation is shown in Figure 2.9 with one of the possible paths selected.

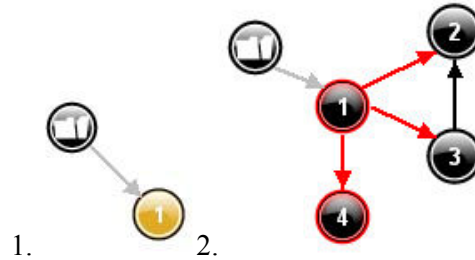


Figure 2.9: 1. Initial states of the U-tube simulation.
2. Complete state-graph of the U-tube simulation.

In the value histories, shown in Figure 2.10, the circles containing the arrows represent the quantity value of the quantity space in each of the states. The arrow indicates whether the derivative is increasing, stabilizing or decreasing and the circle itself represents the magnitude of the quantity.

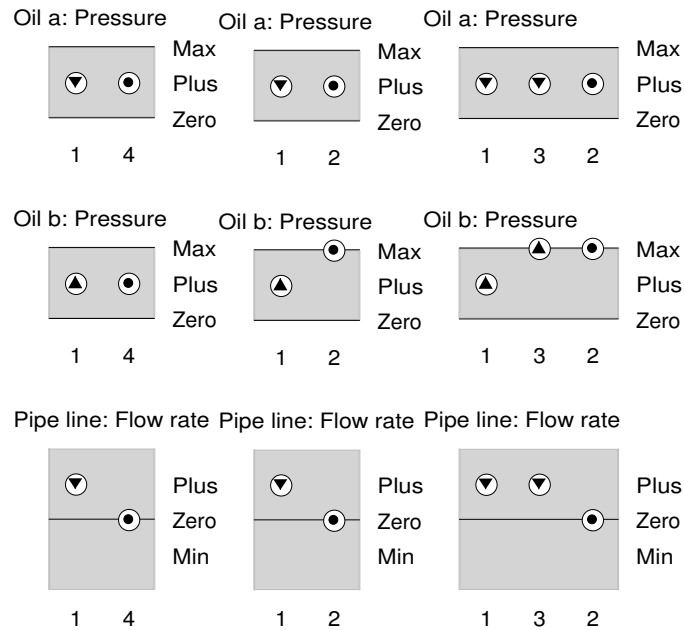


Figure 2.10: Value histories of the various behaviour paths of the U-tube simulation.

From the Figure, it is clear that the Amount of oil in tank A first decreases and then stabilizes, the oil in tank B increases and then stabilizes and the flow goes from tank A to tank B and then stabilizes. The values of the Amount and Level quantities of both oil instances act in the same way as the Pressure quantity and are therefore left out of Figure 2.10. Although this is only a simple evaluation of the results, this represents the behaviour that was predicted correctly.

As shown in the Figure, there are multiple possible behavioural paths, namely {1,4}, {1,2} and {1,3,2}, let's call them respectively, path 1, 2 and 3.

In path 1, the magnitudes of the Pressure quantity spaces stay Plus. The pressure in the target container increases and the pressure in the source container decreases, and although the values have changed, there

is no transition in the quantity space before both pressures stabilize. The flow rate is positive and decreases and stabilizes in zero, describing that there is no flow.

In path 2, the general behaviour is the same as in path 1. The pressure of container b, the source container, decreases, but the pressure rise in container a, the target container, causes a transition in the quantity space, going from plus to max and then stabilizes. The behaviour of the flow rate is exactly the same.

In path 3, there is an additional state between states 1 and 2. This path represents another possibility of the system behaviour, that when the transition from Plus to Max is made, the pressure keeps on rising for a while. Meanwhile the pressure of container A is still decreasing, but will not make the transition towards zero. Eventually, the end state of this path is the same as path 2, and all quantities stabilize.

The difference in behaviours between path 1,2 and 3 can be explained by the fact that the relative size of both containers is never specified in the model fragment library. It is specified that the pressure of container A is greater than the pressure in container B, but not that container A is bigger, smaller or equal in size, so Max in pressure of container B, might be equal to Plus in pressure of container A. The reasoning engine just tries all possibilities that do not contradict the conditions found in the model fragment library.

Another useful tool to inspect the state-graph, next to the value history, is looking at the dependencies of a particular state in the state-graph. In Figure 2.11 the dependencies in state 1 are shown. This is the internal representation of the dependencies that interact between all quantities attached to entities of the u-tube system in the reasoning engine. It is clear that this representation is consistent with the model that was intended.

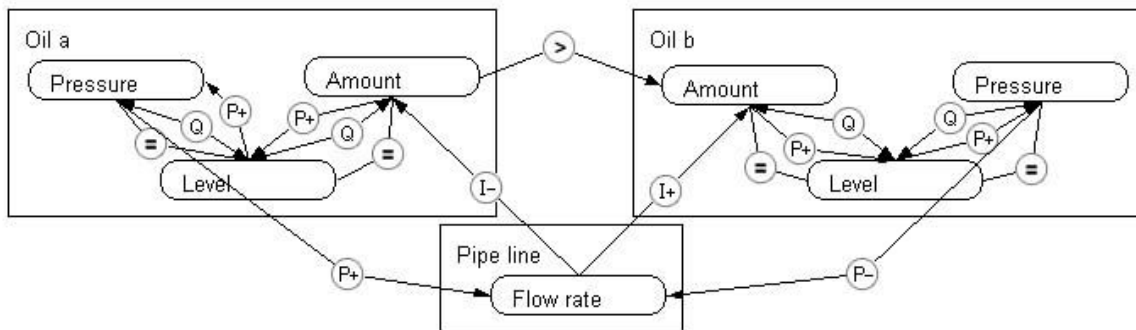


Figure 2.11: The dependencies in state 1.

The Figure shows that the model fragments are added correctly to the system structure and adds the initial condition, set in the scenario, which says the Amount of container a is greater than the Amount of container B.

Garp3 implements several other features to allow users to do more thorough investigation of the simulation results. These features create the possibility to determine if the model captures the real life system and its behaviour correctly, by enabling the user to inspect all qualitative aspects of the derived behaviour.

2.3.7 Simulation preferences in Garp3

It is possible to change some settings in Garp3, which are called the simulation preferences. These settings have influence on how some calculations are executed and the results of the simulation. One of these settings used in this thesis later on, is: *Remove inactive quantities*. This setting implies that whenever from an old state a new state is produced by the reasoning engine, where the new state includes less quantities than the old state (for example because other model fragments are added to the model), the quantities that are inactive will be removed from the model.

2.4 Summary

The notion of common sense reasoning has motivated AI scientists to find ways to formally represent knowledge in a qualitative way, which reduces the complexity of gathering and analysing quantitative data but retains the ability to reason and make predictions about the behaviour of the system.

Qualitative reasoning and modelling enables domain experts to formalize their knowledge into model fragments containing parts of a system structure, built out of modelling primitives. Together these model fragments form a library that contains qualitative knowledge about the system structure and how the system changes under certain conditions. Model fragments can contain building blocks, which are static properties of the system, and dependencies, which describe what influences exist in the system and how changes come to pass.

Garp3 is a software tool, which enables these domain experts to create a model fragment library about a particular system. When the model fragment library is complete, it can be read by the reasoning engine and with a starting condition, which is called a scenario, a graph of possible behavioural paths can be created. These paths consist of states that describe the system during a particular moment in time. Each state is unique, and paths of behaviour can cross each other or split to form other paths leading to other states. Together the paths form possible system behaviour, which can be analysed in different ways to validate the model correctness.

3 Ecology Theory

3.1 Introduction

The ecology domain includes many complex real life systems, which exhibit behaviour that can be observed and analysed. Ecologists have observed these systems for centuries and the results of their observations have led to several notions and proven laws about how ecological systems function. To gain insight into the basic principles underlying food web systems especially the laws and facts about population and community dynamics are important. In this chapter, this knowledge is approached from a process centred view, which means the focus is on which processes cause change and how processes influence each other.

Much of the knowledge captured in this chapter is basic knowledge to experts of the domain and comes from the same source, 'Biology' by Campbell & Reece, 2002, which is a textbook for Biology students.

3.2 Populations

In the natural world surrounding us live many different populations of species. A population is defined as a group of individuals of the same species, which are capable of interacting with each other in a localised area. Furthermore, members of this group need the same kind of resources, will be likely breed with one another and are influenced by the same environmental factors.

3.2.1 Population attributes

Populations have certain attributes and characteristics that define the way they grow and interact with the environment.

Size and Density

To start with, size is used to describe the amount of individuals that are part of the population. The definition of population density is the number of individuals per unit area or volume. Through births, new individuals will be added to the population, and size and density both will increase. Deaths of individuals will decrease population size and density. When the density or size increases, the number of individuals that can reproduce also increases and thus a population is bound to grow faster. This also works the other way around. When the density or size decreases, the number of individuals that can reproduce decreases also and thus population growth will slow down.

Biomass

Sometimes it is needed to express population size in biomass. Biomass is the total mass of living organisms within a specified area. Biomass can be used to compare species populations with low body mass per individual to species populations with higher body mass per individual. The biomass furthermore represents the energetic value of the population and how much energy the population needs to grow or sustain itself.

Changes in a population's biomass occur in the same fashion as density and size. When new individuals are added to the population, the biomass will increase and when individuals die, the biomass will decrease. Biomass however, is more complex than that. Any individual organism has its own biomass value and there will be differences between individuals of the same population. Also, over the course of an organism's lifetime its biomass will change when the organism grows from newborn to maturity and eventually death. This actual increase or even decrease of an individual's biomass is a slow process. Most changes in individual biomass cycle between seasonal events and are thus temporary. Some species will grow fat before winter settles in order to survive and pregnant females will have more biomass when they carry a child.

The real difference between size and biomass can be expressed in the nature of the variables: births will add to the population size one individual at a time while the process of reproduction will add to the biomass gradually from the beginning (from pregnancy to the birth itself).

Birth and Death

Population growth is defined as the change in population size from one generation to the next. Decrease or increase of a population's size or density happens through two processes that are essential to living organisms. Birth, also called *natality*, causes new individuals to be born and thus the size of the population to increase. Birth will be defined here to include all forms of reproduction. Among individuals with the ability to reproduce (mostly females) within the population, birth rates can vary. The variation mostly depends on age. The second process that influences density is death, also called *mortality*, and causes individuals to die and thus the density of the population to decline. Like birth rates, death rates also vary among individuals within a population. These depend on both age and sex.

Immigration and Emigration

Two other processes can also influence the density of a population. Immigration is the influx of new individuals from other areas in the environment and will increase population size and density. Emigration is the movement of individuals out of a population and will decrease population size and density.

Reproduction and Survival

There are two kinds of reproduction: big-bang reproduction, also called *semelparity*, and repeated reproduction, also called *iteroparity*. Big-bang reproduction takes place when an organism creates thousands of eggs or seeds in one single reproductive opportunity and then dies. Repeated reproduction is when organisms take time to mature and then at a regular interval of time reproduce in limited amounts. The amount of offspring, seeds or eggs varies with the species.

Evolution determines whether a population of species favours big-bang reproduction or repeated reproduction. The most critical factor in this is the rate of survival of the offspring. If there is a poor or inconsistent chance of survival, repeated reproduction will be eventually favoured over big-bang reproduction by the process of evolution.

The evolutionary concept of fitness is not measured by how many offspring are produced in one attempt, but by how many survive to produce their own offspring. The age on which an organism is able to begin reproducing, the amount of offspring is produced each time an attempt is made, and how many times offspring is produced during the organism's lifetime are all variables that determine the success of an organism's reproduction. Although, according to evolution theory, the fittest will survive, it's not possible for natural selection to maximize all these variables simultaneously. Organisms live in a world of finite resources, and the limits of these resources means that trade-offs have to be made. Resources like energy, nutrients and time can only be used once, creating a trade-off between survival and reproduction.

Habitat

Habitat is the specific area or environment in which a particular type of plant or animal lives. It must provide all the basic requirements for survival, such as food, water, shelter, and living space. The term can be used to define a population's surroundings on almost any scale.

3.2.2 Population growth

The most important aspect of studying populations is how they grow and decline and what influences these changes in size.

The basic process of growth

The actual growth rate of a population, in numbers of individuals, is the birth rate minus the death rate. In this case there is a positive feedback of the population size or density to the birth and death rates. When the population grows in size, there will be more individuals with the ability to reproduce and more individuals with a real chance to die. With other words, birth and death rate increase when the population size increases. However, in most populations individuals cannot reproduce until they reach a certain age and thus cannot contribute to the rate at which births affect the population size until they reach maturity. The same goes for the death rate, young are less likely to die or sometimes more likely to die. Death rate

is not the same for individuals of a population of different age or sex, since age and sex influence size and ability to protect one self.

To make modelling of the growth process easier and more valid, the birth and death rates can be expressed as the average number per individual of the population during a specified time interval. Births expressed in this way are called the per capita birth rate and deaths expressed in this way are called the per capita death rate. The difference with the original way of expressing births and deaths (as the total number of occurrences) is that it's not necessary to think of the difference amongst individuals in age that implies differences in their chance of reproducing or dying. When there is a population of size A , and there are B occurrences of death or birth during a specific time interval, the per capita death or birth rate for any individual is A/B .

The per capita growth rate of a population is the per capita birth rate minus the per capita death rate. The positive feedback that occurs with calculations on the actual growth rate in individuals does not apply when calculating the per capita growth rate. Of course, there can be extraneous influences that cause an increase or decrease of the per capita birth and death rates. Without these influences the relationship between both rates and the actual size will remain the same when the population grows. Only the principle of safety in numbers (for some prey populations) might indirectly cause the capita birth rate to increase and the per capita death rate to decrease when the population grows.

Zero population growth is rare and when it occurs it will be in a transition from increase to decline of the population size. Only when (per capita) birth and death rates are equal, zero population growth occurs.

The demographic study of growth

Demography is the study of the vital factors that affect population growth. In demography, in populations without immigration and emigration, there are two key factors that determine changes in population size. The first factor is survivorship, which is the proportion of a group of individuals of the same age followed from birth until death that are still alive at each age. These values can be plotted in a survivorship curve. The other factor is the reproductive rate, which is the productive output from a group of individuals of the same age followed from birth until death.

The exponential model of growth

When a population reproduces under ideal conditions, it grows rapidly, because all members have abundant food and are free to reproduce at their physiological capacity. Under these ideal conditions population increase is called exponential population growth. There is a maximum growth rate for every species, and under these conditions the per capita growth rate can become equal to this rate, called the intrinsic rate of increase.

The logistic model of growth

Indefinite population increase like the exponential model describes, does not occur for any species, either in the laboratory or in nature. There are no real life habitats with unlimited resources. The logistic model of growth states that although a small population that begins growing in a favourable environment and may increase rapidly for a while, its growth process will eventually slow down and may even stop as a direct result of limited resources and other factors. The difference between the exponential and logistic model of growth is illustrated in Figure 3.1.

When a population grows larger, the increased density results in more crowding. Since there is a finite amount of available resources for the population, it becomes increasingly difficult for each individual to satisfy its need of resources for maintenance, growth and reproduction. There is a limit on population growth. This concept is defined as carrying capacity. Ecologists define carrying capacity as the maximum population size that a particular environment can support at a particular time with no degradation of the habitat. Carrying capacity is no fixed value, but one that can change over time with the relative abundance of limiting resources. There are several factors that determine carrying capacity, energy limitation being the most important. Other factors are shelters, refuges from predators, soil nutrients, water and suitable breeding spots.

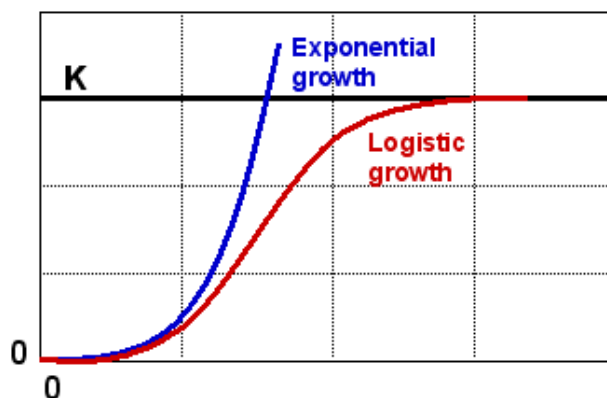


Figure 3.1: Exponential and logistic growth (Campbell & Reece, 2002).

Population growth rate is affected by crowding and resource limitation in several ways. When individuals cannot obtain enough resources to reproduce, the per capita birth rate will decrease. When they cannot obtain enough energy from resources to sustain/maintain themselves, the per capita death rate will also increase. Both these effects will result in a smaller capita growth rate.

In the equation of logistic population growth, carrying capacity is defined as K . The logistic growth model states that a population grows most rapid when it is at some point below carrying capacity and that the growth slows down as the size approaches K . Growth is fastest at intermediate population sizes when there are quite some individuals capable of reproduction and enough available space and other resources in the environment. It furthermore states that birth rate will decrease and death rate will increase when size approaches the carrying capacity. Why this happens can have several reasons and will be elaborated further on in the section on regulation.

Natural populations

In nature, many populations grow approximately in logistic fashion, but there is rarely a stable carrying capacity. Carrying capacities vary among habitats and can vary in space and time. The logistic model assumes a negative effect of increasing size and density, but in nature it is often observed that a greater number of individuals has a positive effect on population growth, up to a certain point.

Also, lag times are observed in natural populations before limiting effects on population growth. For example when food becomes a limiting resource, reproduction will be reduced, but the birth rate may not decrease immediately because individuals may use the energy reserves they have to continue reproducing for a short time. A population can overshoot the carrying capacity because of this lag time. This results in deaths exceeding births and a decrease in population density. Even though reproduction begins again when the population size drops below carrying capacity, there is a delay until birth rate, the actual appearance of new individuals, climbs up again.

Regulation

It's clear that no population can increase forever. There must be regulatory processes that cause birth rate to decline and death rate to increase and a population to return to its equilibrium. What causes these processes to operate?

When immigration and emigration are ignored or offset each other, then a population increases in size when the birth rate exceeds the death rate and declines when the death rate exceeds the birth rate. Population growth will not stop without negative feedback between population density and the vital rates of birth and death. The decrease of birth rate and increase of death rate to slow down growth can occur under the influence of density. A death rate that rises as population density rises is said to be density dependent, as is a birth rate that falls with rising density. Density independent birth and death rates do not react to changes in density. Density dependent and independent rates are illustrated in Figure 3.2. For a population to persist, it is required that density dependent processes take place. Population persistence is the ability to continue to exist over a period of time.

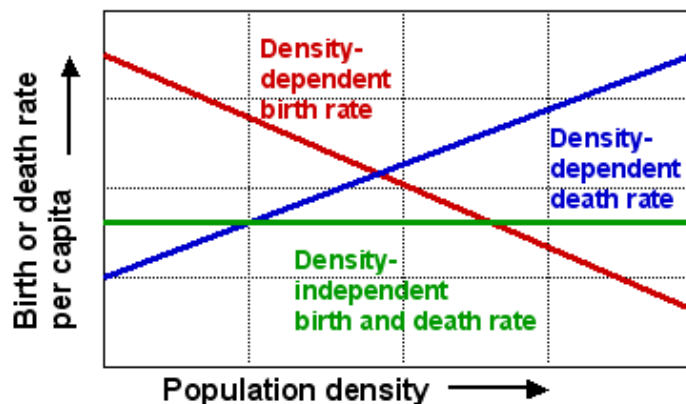


Figure 3.2: density dependent processes.

There are several examples of density dependent feedback that will cause populations to stop growing.

- When the amount of available resources becomes scarce intra-specific competition for the declining nutrients may ensue. When a population gets more crowded reproduction may be reduced because every individual gets a smaller share of nutrients.
- Territoriality restricts population growth when there are only so much suitable breeding spots. When density increases there will be individuals that will not succeed in securing such a spot and will therefore not reproduce.
- When density increases some individuals of a population remain smaller than others. Their chances of survival are smaller than those of other individuals of the population.
- Predation can be a cause of density-dependent mortality for some prey populations. Predators will capture and eat more prey when the population density of the prey increases.
- Accumulation of toxic waste can also cause density-dependent mortality. This is sometimes observed in laboratory conditions. Some metabolic by-products accumulate as the population grows, poisoning the population itself.
- The impact of diseases can be greater when density is higher. When there is more crowding it is possible for a disease to spread faster and further than when density is low.

3.3 Communities

A community consists of all the organisms of all the species that inhabit a particular area; it is an assemblage of populations of many different species. The composition of species within a community defines its properties and the interactions between the species defines the structure of the community. Between different communities there are huge differences in species richness, the number of species they contain. Also, species can differ in their commonness, creating differences in the relative abundance of species between communities.

3.3.1 Community composition

There have always been arguments among ecologists on why and how communities are composed. There are two historic hypotheses about community composition that are forerunners of the more recent community models. *The individualistic hypothesis* of community structure proposed by H.A. Gleason, says it is chance that a plant community is composed the way it is. The species found in the same area are simply there because they have the same abiotic requirements. *The interactive hypothesis* proposed by F.E. Clements, says that the biotic interactions between species, that cause a community to function as an integrated unit, determine the assemblage of the community. The individualistic hypothesis is commonly accepted by plant ecologists, but there is still argument about the application of these ideas to animal communities.

There are two models proposed to explain the way species in a community are linked together. *The rivet model* suggests that there is a web of life that connects most of the species tightly with other species. This implies that the increase or decrease of one species in a community affects many others (P. Ehrlich and A. Ehrlich, 1981). *The redundancy model* assumes that the web of life that connects most species in a community is very loose and that most of the species are not tightly associated with each other. This implies that reduction or increase of the abundance of one species in a community has little effect in other species, which live independently (Brian Walker, 1992). These two models represent extremes and most communities will lie somewhere in the middle of these two models.

3.3.2 Interactions between species

In table 3.1 an overview is given of the most important inter-specific interactions. These interactions are relationships between the species of a community.

Table 3.1 Interactions between species in a community.

Interaction	Effect on Population Density
Competition (-/-)	The interaction is detrimental to both species
Predation (+/-)	The interaction is beneficial to one species and detrimental to the other.
Mutualism (+/+)	The interaction is beneficial to both species
Commensalism (+/0)	One species benefits from the interaction but the other is unaffected

Competition

When two species need the same limited resource or resources there is a potential for competition between them. If there is competition for a resource one or both species can suffer reduction of their population density or one can become extinct. The competitive exclusion principle states that even a small reproductive advantage of one competitor over another will lead to local extinction of the inferior species (R.F Gause, 1934).

When looking at a species' ecological niche, the competitive exclusion principle can be restated. A species' ecological niche is the sum total of a species' use of the biotic and abiotic resources in its environment. If the niches of two species are identical, they cannot coexist in a community and one of them will be eliminated according to the competitive exclusion principle. However, when two ecologically similar species have one or more differences in their niches, they can coexist in a community.

Resource partitioning is a result of the evolutionary process that differentiates the niches of similar species and enables them to coexist in a community. One of the competitors adapts in such a way that competition becomes obsolete. This is one possible outcome of competition, the other is (local) extinction of the inferior species.

Predation

The act of one population of species using another population of species as source of food is called predation. Predators wholly rely on killing and eating their prey for nutrients. Herbivory, where an herbivore species eats part of the whole of a plant, and parasitism, where a parasite organism lives inside or on its host and depends on it for nutrition, are also considered to be predation by ecologists. Pathogens that cause disease in their host are also parasitic predators, but although most parasites will not kill their hosts, many pathogens can inflict lethal harm.

Predation is an important factor in the evolutionary process because eating and trying not to be eaten are needed for reproductive success. Predator species have many abilities that enable them to locate, find and catch their prey. Prey organisms have adapted to being preyed upon by defending themselves in several ways, making it more difficult for the predator to catch and eat them and improving their own chances of survival.

Cycles in population size also result from a time lag in predator prey interactions. Most predators have a greater body size and reproduce more slowly than their prey. When prey numbers are rising the predator lags behind their population growth. Lokta-Volterra's law further extended by Berryman in 2003 says that

negative feedbacks between a population and other species or even components of their environment, are likely to result in oscillatory dynamics (Haemig, 2005) as shown in Figure 3.3.

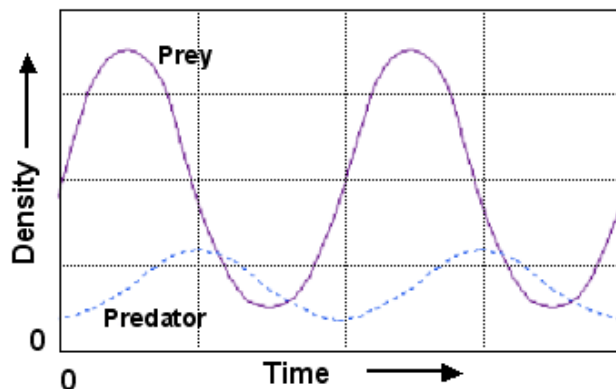


Figure 3.3: Oscillatory dynamics between predator and prey.

Mutualism

This inter-specific interaction benefits both participating species. Mutualism or Mutual Symbiosis means cooperation between two species, which results in beneficial effects to both species. An example is an ant population that feeds on the by products of a plant and finds shelter in the plants foliage while simultaneously defending the plant from other insects and removing fungal spores and parts of other plants growing near to it.

Most mutualistic interactions have evolved from predator-prey or parasitic relationships.

Commensalism

Commensalism is an interaction between two species with only one of them deriving benefit from it. Examples of such an interaction are algae that attach to the shell of aquatic turtles. These are called hitchhikers. But it may also be that these species reduce the efficiency of movement of the species they're attached to.

3.3.3 Community structure

The feeding relationships between organisms in a community mainly determine its dynamics and structure. This structure is called the trophic structure of the community. A food chain is ordered from begin to end according to the direction in which food and energy are flowing from its source in plants and other photosynthetic organisms to eventually the decomposers that break dead matter down into soil nutrients.

Trophic theory

In a food chain several trophic levels can be distinguished. In the first trophic level the photosynthetic organisms, such as plants, can be found. They are called the primary producers. The second trophic level consists of herbivores, species that feed on plants. These are called the primary consumers. The third and fourth trophic levels extend to mostly carnivorous predators and parasites. These are called the secondary and tertiary consumers. An overview of the trophic levels is given in table 3.2.

Table 3.2: An overview of trophic levels.

Trophic level	Contains	Trophic layer
1	Photosynthetic organisms: plants, photosynthetic plankton.	Primary producers
2	Herbivores: organisms that feed on photosynthetic organisms	Primary consumers
3	Carnivores and parasites that feed on herbivores.	Secondary consumers
4	Carnivores and parasites that feed on other carnivores or parasites.	Tertiary consumers

There are two well known hypotheses about community structure and regulation through trophic levels. The tri-trophic Green World Hypothesis (GWH) (Hairston et al., 1960) first identified trophic levels. With their hypothesis that predators maintain global plant biomass at high trophic levels by limiting the densities of herbivore populations, Hairston et al. started 40 years of debate in the ecological world. They state that predators and parasites control herbivore populations top down. According to Hairston et al. this was the reason that the world was green. Herbivore densities remain low as a result of top-down control of predators and allow plants to grow unimpeded by predation (Polis et al., 2000).

Another hypothesis is the exploitation ecosystem hypothesis (EEH) (Fretwell and Oksanen et al., 1981). They propose a conceptual framework of 'exploitation ecosystems' where strong consumption leads to alternation of high and low biomass between successive levels. When herbivores graze on plants only a little of the energy that is captured in plants passes directly into the next trophic level. Herbivores gain about 10% of the energy fixed in the productive level of plants, the rest passes into the detrital chain (Polis & Strong, 1996). The energy distribution between trophic levels is illustrated in Figure 3.4.

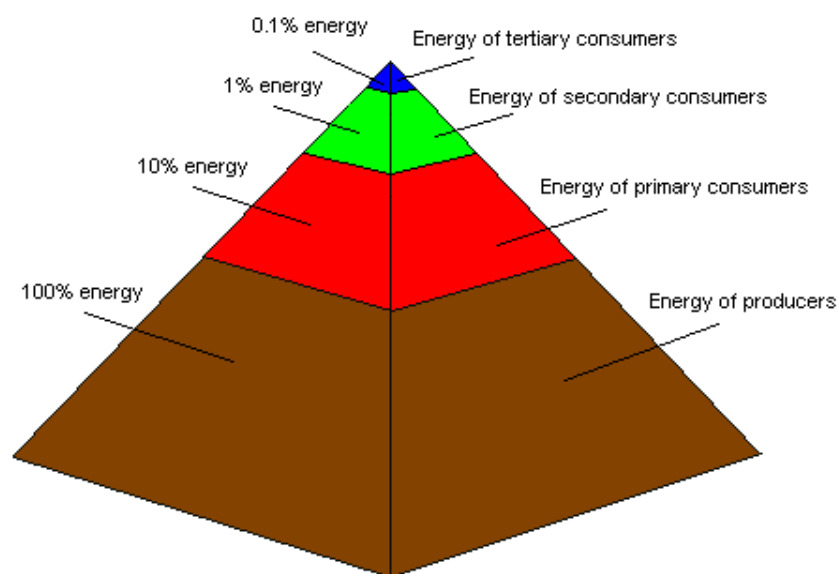


Figure 3.4: Energy distribution between trophic levels.

Dependent on the productivity of the habitat, the EEH model assumes a number of 'effective' trophic levels. A level that is not limited from above but limits the level below it is an effective trophic level. This suggests a potential number of links energetically possible in a food chain dependent on the productivity of the habitat (Ayal et al., 1999).

Food webs are very complex systems and both the GWH and EEH suggested that, to simplify these systems to study general patterns in real life natural systems, species with similar feeding interactions could be put in the same discrete trophic levels (Polis et al., 2000).

Food chains and webs

Trophic levels determine how food chains are ordered and explain the interactions between species on different positions in a chain. The amount of trophic levels a food chain can contain is limited to only four or five links. But communities cannot be simplified into just food chains. Food chains are not stand alone units but are hooked together into food webs. These are very complex webs linking many species by their feeding relationships (Elton, 1920).

There are two aspects of species in a chain that transform food chains into food webs. Firstly, some species can be active at more than one trophic level. Omnivorous organisms can be both primary consumers and secondary consumers in a food web. Secondly, most consumer species are nonexclusive. Consumers feeding on multiple prey species that are located in different food webs, link these food chains

together in a web. But not every carnivore node in a food chain can be connected to any other. A predator may change its diet from some prey to another when there is a need but there is a limit on the size of food any animal can eat. Also, larger carnivores cannot live on much smaller prey because there is a time limit in which the predator needs to fulfil its metabolic needs (Polis & Strong, 1996).

Although food webs are complex systems, they can be simplified in two ways. First, there are broad taxonomic groups that group species together when their trophic relationships in a community are similar. Secondly, some parts of the web that interact very little with the rest of the community can be isolated from the rest.

Limiting factors on food chains

There is a limit to the length of the food chains found in a food web. There are two hypotheses why the length of food chains is limited to a few links.

The most widely accepted explanation for food chain length is the energetic hypothesis. There is an inefficiency of energy transfer along the chain that limits the length. From every trophic level in the chain only about 10% from the energy stored in the organic matter passed along to organic matter in the next level. Because the initial availability of resources in every habitat is limited, there is a limit to the length of any chain that extends from producers in a habitat.

There is also a relationship between food chain length and the size of a habitat. Larger habitats support larger taxonomic groups of species and food chains lengthen with habitat volume (Power & Dietrich, 2002).

Productivity is never high enough to support more than three effective levels on land and four on water (Oksanen et al. 1981; Oksanen 1988). But it is also argued (Hairston and Hairston, 1993) that physical differences between habitats cause three levels on land and four on water (Polis & Strong, 1996).

The dynamic stability hypothesis has an alternative explanation for the limited length of food chains. Stability decreases when chains grow longer. A short food chain is more stable than a long one according to this idea. Changes in abundance in lower trophic levels are magnified at higher levels, making top predators vulnerable to extinction when the chain lengthens. Also the recovery rate from environmental setbacks for top predators will be slower when the chain is longer.

3.3.4 Food web dynamics

As mentioned earlier, food webs are very complex systems. This also means that behaviour of these systems is increasingly difficult to predict. There are several factors that can be pointed out to illustrate the complexity of food webs.

Link strength

Not all nodes in the web or even in a chain have the same impact on the whole.

There is a difference between donor controlled links and recipient controlled links. In donor controlled links the consumers do not affect the renewal rate of the resource they feed from. In recipient controlled links the consumers do affect the renewal rate of the resource they feed on. A consumer often has higher chances of persistence by eating resources whose abundance they do not influence (Polis & Strong, 1996).

Complexity and stability

It is suggested that complex systems are more stable than less diverse systems (Polis et al., 2000).

The high connectance in food webs diffuses direct effects of consumption and productivity across multiple trophic levels. The dynamics of individual links is not only affected by the interactions with the trophic levels directly connected to them, but also by species multiple position along the trophic spectrum. This increases the complexity of web dynamics considerably (Polis & Strong, 1996).

However, about this effect of interconnections on food web stability many things remain unknown, which makes it difficult to make models of food webs that extend linear food chains (Jefferies, 2000).

The availability of inorganic resources

It is argued that inorganic nutrients and water, which are crucial for plant abundance, are central to web dynamics. They determine the productivity of the first trophic level and the strength of bottom up effects. However, productivity does not directly increase with nutrient availability, so the commonness of nutrients and water do not serve as explanations for food web variation (Polis & Strong, 1996).

3.3.5 Community structure control

It is evident that populations in communities influence each other and that changes in one population can affect populations much higher or lower in the trophic structure of the community. There are several theories of how communities are organized.

Keystone species and dominant species

There are certain species in that may have a larger impact on the entire community than other species. Those species are either dominant or keystone species. Dominant species have the highest abundance or highest biomass in a community. Because of this they have control over the distribution and occurrence of other species. The control on community structure that keystone species have is more dependent on their ecological role, or niche.

Bottom-up or top-down control

There are two models of community organization that ecologist distinguish between: The bottom-up model that is controlled by nutrients and the top-down model that is controlled by predators.

To clarify these models, there are three kinds of possible relationships between vegetation V and herbivores H.

$$V \rightarrow H \qquad V \leftarrow H \qquad V \leftrightarrow H$$

The meaning of the arrows is a change of biomass in one trophic level also causes a change in the other trophic level.

To begin with the bottom-up model, it exists of $V \rightarrow H$ linkages. The community organization is controlled by mineral nutrients that control up to a point the plant numbers, which in their turn control herbivore numbers etc. If this model is correct all trophic levels should increase in biomass when mineral nutrients are added so that the vegetation will grow. When predators are added or removed this will not have any effect for the lower trophic levels.

The top-down model exists mainly of $V \leftarrow H$ linkages. The community organization is controlled by predators that control herbivores by predation P, which in turn control plants by predation. A simplified version of the top down model is: $V \leftarrow H \leftarrow P$. This model is also called the trophic cascade model. It is assumed that the effects of manipulation at the top will move down through the trophic structure inverting abundances. Earlier mentioned GWH is an example of a top-down model (Polis & Strong, 1996).

There is variation in the degree in which real life communities fit to the models of top-down and bottom-up control.

Trophic cascades

A trophic cascade is a rare phenomenon that occurs when there are sudden or huge changes in densities of higher trophic levels of food chains or webs. It is a chain-reaction that moves down the chain shifting the dominance and impact of consumer levels lower in the food chain or web. Species abundance can be inverted across more than one trophic level. An example would be a three layered food chain and the top predator increasing in density. The result could be a lower abundance of the herbivore consumer level and a higher abundance of plants.

A distinction between species level cascades and community level cascades can be made (G.A. Polis, 1999). Species level cascades occur usually within a subset of the community in such a way that changes in abundance of a predator only affect the abundance of a subset of the plant species. Community level cascades can substantially change the distribution of plant biomass in the whole community (Polis et al., 2000).

3.3.6 Disturbances

There are some natural and unnatural events that damage communities, remove organisms from them and alter the availability of resources. Examples of these disturbances are storms, fire, floods, droughts, overgrazing or human activities. It is suggested that most communities have some amount of non-equilibrium from disturbances that have taken place. Communities can recover slowly from these disturbing events and they're mostly in some state of recovery from disturbance.

3.4 Environment

An environment consists of both abiotic components and biotic components. Abiotic components are those factors that are nonliving chemical and physical like temperature, light, water and nutrients. Biotic components are the living organisms that share the environment.

3.4.1 Abiotic factors

- *Temperature* is an important factor for organisms and their distribution because it affects biological most processes. Most organisms cannot regulate their body temperature precisely and are therefore dependant on the right variation in temperature.
- *Water* is essential to all life on earth, but varies greatly in its availability among different habitats.
- *Sunlight* is the source of the energy that provides all organisms within an ecosystem by flowing through the various trophic levels. Only photosynthetic organisms such as plants and some kinds of bacteria can use this energy source directly. The light itself is also important for the many species that rely on photoperiod to cue some of their behaviour and development. Photoperiod is the relative lengths of daytime and nighttime and is more reliable than temperature to indicate a change of season and required accompanying events like migration by animals.
- *Wind* is an important factor because it amplifies the effects of temperature on organisms by a mechanism also called the wind-chill factor. This process causes organisms to loose more bodily heat due to evaporation and convection.
- *The physical structure, acidity, and mineral composition of rocks and soil* is limiting to the distribution of plants and those animals that feed upon plants.
- *Climate* determines the local weather conditions in an environment and is composed of the four major abiotic factors; temperature, water, light and wind.

3.4.2 Energy flow and chemical cycles

The trophic level of primary producers or autotrophs consists of organisms that can support themselves and ultimately support all other organisms in the ecosystem. Organisms in trophic levels above the producer level are called heterotrophs and depend directly or indirectly on the photosynthetic output of the primary producers. Detritivores, or decomposers, are an important group of heterotrophs. They get their energy from non-living organic material, like the remains of dead organisms, fallen leaves and wood, also called detritus. Although the level of decomposers is most commonly ignored when looking at food web dynamics, their role is crucial to matter cycling in ecosystems. In a way decomposition connects all trophic levels and makes it possible that matter keeps on cycling within an ecosystem. Energy, from the sun as external source, flows through all the trophic levels of an ecosystem rather than cycling like matter. At the end of every trophic level, energy is vented off as heat that biomass produces like shown in Figure 3.5.

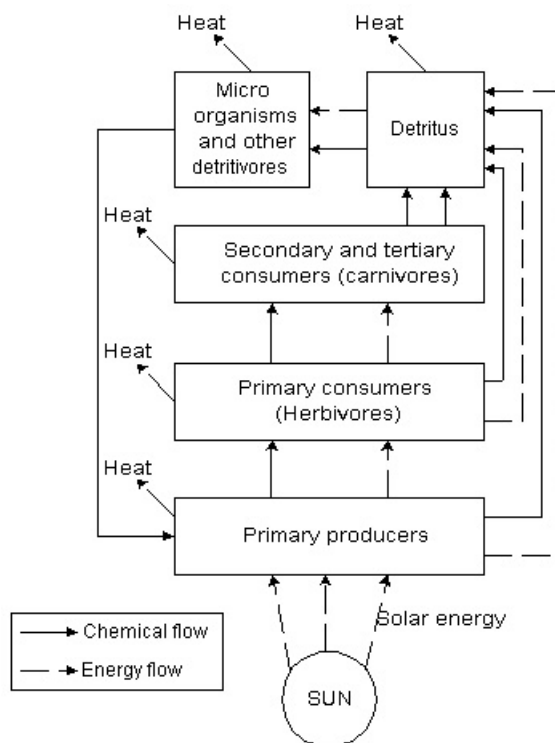


Figure 3.5: Energy and matter cycles in the trophic structure.

3.5 Summary

Individuals of one species are grouped into populations with internal dynamics, which can be generalised for any possible population. Populations of different species grow and behave in the same way and although they may have different trophic roles, their internal dynamics are comparable. The trophic role of a species determines how the population gains its resources such as energy and nutrients.

Interactions between different populations also create behaviour that can be generalised for any two populations. The way this behaviour is propagated through the chain or web is an aggregate of many of these interactions and the roles the links have in the chain or web. The domain and the way the important concepts are linked together, are captured in the concept map shown in Figure 3.6.

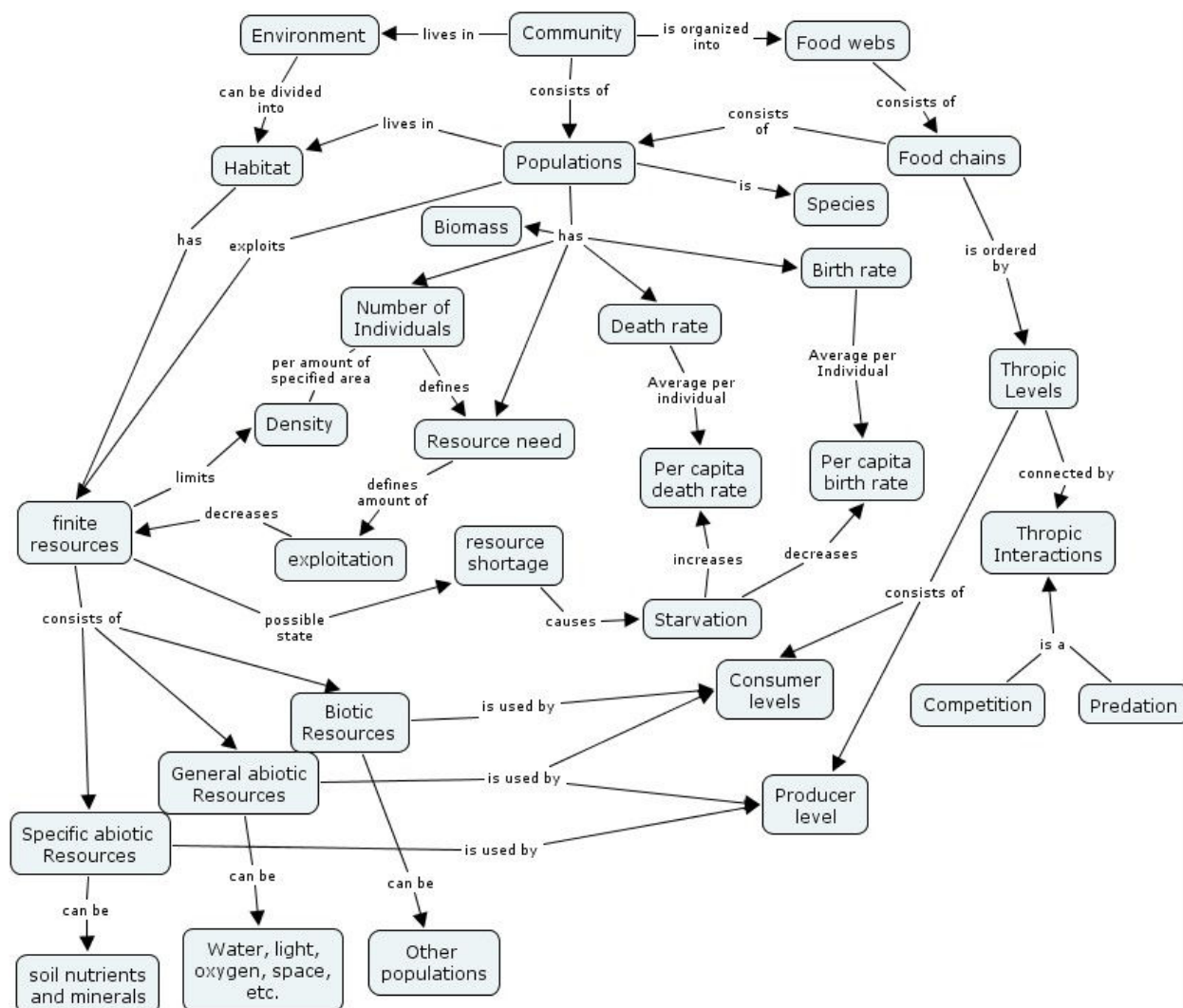


Figure 3.6: Community domain concept map.

Simplified, food webs can be separated into three levels of complexity. The first level consists of the internal population dynamics of every population of species that is included in the web. The second level regards populations as a whole rather than comprising out of several properties and focuses on the dynamics of interactions between populations in the hierarchy of trophic levels. The third level of complexity considers all these interactions as parts of one system and includes the whole food web.

4 Modelling the single population

4.1 Introduction

The modelling task is to create a correct and reusable model of a single population. In order to create this model, the single population dynamics, identified in the previous chapter, are extensively studied and analysed to specify a formal description of the single population. Then this formal description is transformed into a qualitative model. The construction of the formal description and the qualitative model is constructed by following the methodology developed in the NaturNet-Redime project (Bredeweg et al., 2005). In this way it is assured that every modelling choice will have a valid motivation and that the model and simulation results are evaluated.

4.1.1 The single population

There is a population living in an environment. The environment replenishes its available resources at a constant rate and because of this, at a particular time, a certain amount of resources is available in the environment. These resources are nutrients, area with sunlight, water and space. The population grows on the resources, defining it as a photosynthetic organism capable of increasing its biomass and producing offspring by taking up nutrients and water from the soil and energy from sunlight. It is assumed that the world is favourable for the single population, which means that births exceed deaths until the world ceases to be perfect and introduces a factor that increases the number of deaths.

A populations' birth rate increases when there are enough available resources in the environment. This means that the population uses some part of the available resources and will use more as the population grows, because bigger populations need more resources for sustenance, individual growth and reproduction. The size of the population sets the required amount of resources and can also be used to determine whether there are enough or not enough resources for the population to grow.

Because of the assumption that this population has no natural enemies in the environment it can only die by natural causes, like old age or the regulatory processes that will occur when there is a shortage of resources. When growing unimpeded it will eventually reach a size where it needs more resources than the environment can supply. This is when regulatory processes will cause negative feedback that will slow down population growth.

Due to this negative feedback from resource shortage, deaths will exceed births and the population size will decline. When the population size reaches a level where the environment can sustain it again, negative feedback will decrease. The replenished available resources cause birth rate to increase and death rate to decrease and will allow births to exceed deaths again, which will result in growth of the population.

4.1.2 Modelling goal

The goal of this modelling task is to construct a compact model of a single population, which gives insight in the concepts underlying the theory and can be reused when modelling the interactions between populations.

4.2 Creating the causal model

In chapter 2 it is stated that the modelling task begins with the construction of a library of model fragments. A causal model can help to identify the modelling primitives that need to be implemented in the modelling task of a complex real life system. A causal model is a diagram, which regards the causality of the whole system, using primitives from the formal language of modelling primitives explained in chapter 2. To create this model, first the important processes in the single population system are identified. Then choices are made about how these processes are best described using qualitative modelling primitives. The causal model is then constructed from these modelling choices and explained by giving a prediction of the model behaviour by looking at the captured causality.

4.2.1 Processes in the single population

The single population dynamics can be divided and organized into several processes that depend and interact on each other. These processes and the system elements to which they are attached, together make up the system structure.

Birth: every population has a birth process, the process of reproduction that adds new individuals to the existing population and causes an increase in the size of the population. The total birth rate within a population is influenced by how many individuals are capable of the act of reproduction and how much resources are available for them. Birth rate is the total number of births that take place in a population on a specific point of time in its existence. The average birth rate per individual of the population is called the per capita birth rate. Birth rates will only become zero when the population ceases to exist.

Death: every population also has a death process. This consists of the sum of the many possible causes of death and their actual occurrences for individuals in the population. Death as a process is influenced by several factors, which are distinguished as the causes of death that can be generalized. Death rate is the total number of deaths that take place in a population at a specific point of time in its existence. The average death rate per individual of the population is called the per capita death rate. Death rates will only become zero when the population ceases to exist.

Population growth: through the processes of birth and death every population has a growth rate. Growth is the birth rate minus the death rate, resulting into the rate with which the population grows in individuals. Growth can become zero when births and deaths are equal or negative when deaths exceed the number of births. When the population is open, the processes of immigration and emigration also exert their influence on the population. Then the calculation for growth rate is births and immigration minus deaths and emigration. Growth can only occur when there are birth and death rates or immigration and emigration.

Sustenance: every individual in the population and the population as a whole needs energy extracted from nutrients and sunlight to maintain its metabolism. Also, for an individual to grow in body size it needs a certain amount of energy. The nutrients and sunlight usage by an individual to grow and maintain itself is called sustenance.

Exploitation of resources: every species needs resources like nutrients, space and water. The process of using, for example by eating them, the resources a population needs is called exploitation of resources. This causes the available resources to decline. Exploitation of resources will only become zero when the population ceases to exist or when there are no more resources.

Regulatory processes: when a population approaches the resource threshold of the environment or habitat, regulatory processes become active. These can be a wide variety of processes, but their overall effect is the same. These processes cause birth rate to decrease and death rate to increase, eventually slowing down population growth or even causing a decline in population size. This negative feedback only occurs when the environment cannot support the size or growth rate of the population. The processes will stop operating when they have caused a decline in population size or growth rate towards a level where the population can once more be supported by the environment.

Immigration and emigration: there are two processes influenced by external factors, which can influence the single population. Immigration works like birth rate, and will add individuals to the population and emigration works like death rate and will decrease the population size because individuals leave the population. Immigration and emigration are only active when there is an assumption, which says that the population is open. Immigration is the only process that is controlled by external factors, because its influence is set solely by the external populations from where individuals migrate into the population.

4.2.2 Modelling choices about the environment

The environment

For simplification it is assumed that an environment has a constant nutrient, energy and water inflow that is inexhaustible. A growing population uses the resources in the environment, such as water in a lake and nutrients from the soil, and as it grows that which it has used is re-supplied at a constant rate.

Modelling resource exhaustion

To simplify modelling the notion of exhaustion of resources by the population, the choice is made to introduce a threshold which is determined by space and (nutrient and energy) resources, which are two out of three factors influencing birth- and death rates. To simplify this even further, space and resources can together be regarded as one limiting aspect, because even when only space or resources is limited, the same consequences are suffered by the population. This threshold is not necessarily a static threshold, it can change when resources are used or added to the environment. The available resources in the environment define this threshold.

The static threshold versus the non-static threshold

When it is possible to determine the amount of resources that is needed by the population, the exploitation of the environment by the population can also be calculated. As explained in the previous chapter, a population uses resources, which depletes the amount of available resources in the environment. However, in the single population model, a static threshold of available resources is chosen which will be called the simple environment.

The focus of the model is on the population dynamics. Although the population needs feedback from the environment to calculate whether the exhaustion threshold is exceeded, a non-static threshold, which represents the result of the inflow of resources minus the resource usage by the population, does not give any additional feedback when compared to the feedback given by a static threshold.

4.2.3 Modelling choices about the population

Using the causal dependency primitives that are introduced in chapter 2, a causal model of the single population can be made. This model describes how the quantities in the model influence and interact with each other. Figure 4.1 shows the causal model of the single population dynamics, which will be explained by the motivation of the modelling choices.

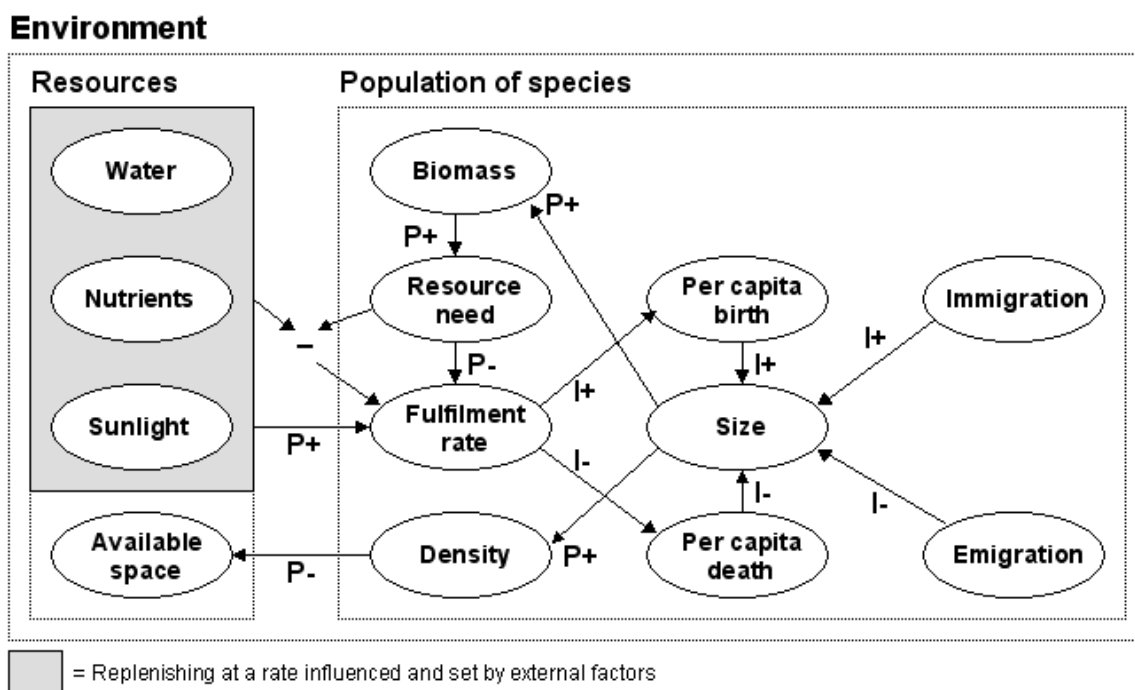


Figure 4.1: Causal model of single population dynamics.

Size, biomass and resource need of a population

Size and biomass are the most important attributes of the population. As explained in the previous chapter, size is expressed in the number of individuals and biomass in the total mass of all individuals. In this chapter a third attribute is introduced which expresses the amount of resources the population needs

at a particular point in time. These attributes are all related, which is also expressed in the causal model. Birth and death processes directly influence the size of the population. The increase or decrease of the size indirectly influences biomass. Since biomass represents the energetic value of the population, this attribute also indirectly influences the resource need of the population because the current energetic value determines how much energy is needed to maintain the biomass.

Space and density

Density is the only attribute of the population that directly influences the amount of available space. It is impossible to determine if space decreases when the size of the population increases, unless information is available about how much individuals occupy one unit area. Density describes this aspect of the population and therefore influences space negatively and will decrease the available space when increasing. When density decreases, available space should increase, but, unless the habitat increases in size, there is only a finite amount of actual space.

However, since the choice is made to regard space and resources together as one limiting aspect, density and space are not included in the qualitative model.

The influences of birth and death

The difference between birth and death rates which change with the population size, and the per capita birth- and death rates, which do not change with rising population size, becomes more obvious when modelling these processes. Modelling birth and deaths in general means that birth rate has a positive influence on the size, causing size to increase and that death rate has a negative influence on the size, causing size to decrease. However, when modelling birth and death rates, population size has a positive influence both rates, because a bigger population has a higher birth- and death rate.

When expressing birth and death as the average number of births and deaths per individual during a specific time interval, these average rates will not necessarily change when the population size changes. Only the direct influences of per capita birth and death on the population size are modelled. Because choosing to model only average birth- and death rates reduces ambiguity considerably when determining the state-graph of a simulation, without losing conceptual correctness, the per capita rates are used. From this point onward, when birth- and death rates are mentioned, the per capita rates are meant.

Modelling growth

Growth occurs when the birth rate is higher than the death rate. When there is no growth, the birth rate is equal to the death rate and they offset each other. This state is called equilibrium. Decline of the population happens when the birth rate is lower than the death rate. When modelling growth, increase or decrease of the population is determined by the equality relation between birth and death rates.

Modelling changes in birth and death rates

Since growth of a population is determined by the equality relation between birth- and death rates, it is important to know how birth- and death rates change and why. It is assumed that populations have an intrinsic per capita birth and death rate, and that birth rate is higher than death rate until the world ceases to be favourable. The world may cease to be favourable by the activation of self-limiting processes, predation by other species or resource shortage etc. These conditions will cause birth rate to decrease and death rate to increase, until eventually deaths exceed births.

Looking at the previous chapter, there are three conditions that can cause changes in birth- and death rates; safety, space and (nutrient and energy) resources. When safety, space and resources increase, as a rule birth rate increases and death rate decreases. The other way around, when safety, space and resources decrease, birth rate decreases and death rate increases.

There are several reasons for the death rate to change. Most deaths are natural like death of old age, stillbirth and accidents. Natural death rate sets the initial per capita death rate of a population. Another cause of death is death by resource shortage like starvation, dehydration, crowding, overgrazing and competition. Another possibility is death by being eaten. This is caused by predation by another population and directly increases the per capita death rate. This also includes death by pathogens or parasites, since these small organisms also live off their host and can cause their death. The last possible

factor which can increase the death rate of a population is death by habitat disturbance like a temperature drop, poisoning, drought, and floods etc. These are rare but possible processes that can wipe out entire populations by increasing the per capita death rate.

There are also factors influencing the capita birth rate. When the conditions resources, space and safety are maximized, capita birth can also be maximized, but these conditions can also limit reproduction and cause a decrease in the capita birth rate. Reproduction takes time and resources. A shortage of resources will cause a decrease in the birth rate. Space can also limit birth rate by the amount of available safe breeding spots for some animals or the amount of fertile soil for plants to grow on. Also, when space is limited, young will get trampled or may die sooner from diseases or waste poisoning. Limited safety only causes an increase in the death rate of young individuals but will not affect birth rate directly.

Modelling the regulatory processes

There can be many types of negative feedback that decrease birth rate, increase death rate or both at the same time. When the threshold of space or resources is exceeded, regulatory processes are caused that increase death and decrease birth rate.

To determine whether the threshold is exceeded, the available resources need to be compared with the resource need of the population. To model the effects caused by the regulatory processes, birth should decrease and death should increase when the threshold is exceeded. Birth and death should stabilize when the need equals the threshold. Birth should increase and death should decrease when the need is below the threshold.

It seems contra-intuitive to make death rate decrease when there is an abundance of resources, and conceptually it is not correct. There is an initial death rate which only increases when the regulatory processes become active, and decreases again to the initial value when these processes stop operating. It is unclear whether it is birth rate that rises and falls with the availability of resources, or death rate. But when looking at the modelling purpose, it is irrelevant whether birth- or death rate changes, or both at the same time. It can be reasoned that births exceed deaths until the regulatory processes become active or predators are introduced, which will cause deaths to exceed births.

Extinction

A population that goes extinct means that the size of the population is reduced to zero. This could happen when there is a long time resource shortage, heavy predation, an epidemic of pathogens or a major habitat disturbance that keeps death rate higher than birth rate for a long period of time. In a closed single population which lives in a closed world without predation, only a long period of time in which resource shortage occurs can cause extinction of the population and make size drop to zero.

Immigration and emigration

When the population is open, immigration and emigration are introduced. In the previous chapter it is stated that immigration and emigration are the only other two processes next to birth and death that can influence the number of individuals of the population directly. When immigration and emigration are added to the model, immigration positively influences size of the population and emigration negatively influences the size of the population.

4.2.4 Prediction of behaviour

The first typical kind of behaviour that can occur is stabilization of the growth rate. This is a sort of equilibrium for the population where it does not deplete its resources but keeps growing at a steady pace. The environment is able to support the growth rate of the population.

The second kind of typical behaviour, is that the regulatory processes will cause the death rate to exceed the birth rate and the population size to decline temporarily. When, because of this temporal decline, the population has reached a level of resource need which again can be supplied by the environment, the population will begin to grow again. This is repetitive process that will cause cycles in the behaviour graph.

Extinction of the population will only take place when there are external influences like a permanent resource shortage or heavy predation that causes the death rate to exceed the birth rate for too long. For

this description of the typical behaviour of a single population, the population is considered to be closed so no immigration and emigration do occur.

4.3 Implementation

The causal model is constructed with theoretic motivations from chapter 3 to validate its conceptual correctness. The next step is to build the qualitative model of the single population. The causal model will serve as the general guideline to implement the causality observed in theory, into a library of qualitative model fragments.

4.3.1 Structural details

Entities

Population: a producer population is capable of reproducing, growing and producing oxygen by using nutrients from the soil and sunlight. Most of the producer species are plants. They provide most of the energy for the upper level species of a food chain. A population can also be a consumer, which means it is a herbivore or carnivore species.

Environment: an environment is the situation in which communities and thus populations of species live. Environments can be further divided into habitats, pieces of environments that meet the specific needs of a population and where a specific population of species lives.

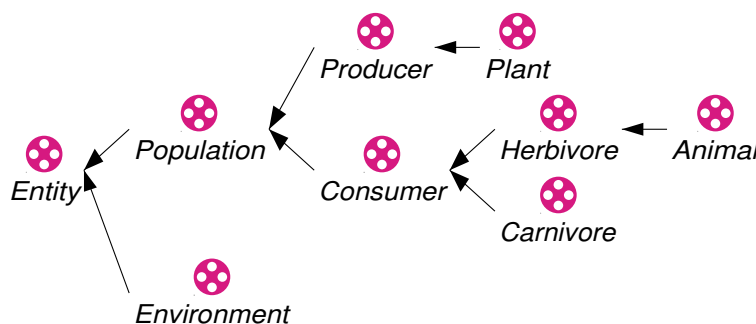
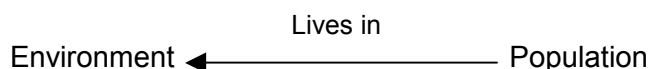


Figure 4.2: The entity relationship diagram of the single population model.

Structural relations



The *lives in* configuration describes that a population is using the environment as its habitat and directly uses the resources available in the environment to sustain itself and to grow.

4.3.2 Quantities and quantity spaces

An overview of all quantities and quantity spaces is shown in table 4.1.

Population quantities

Size – This quantity represents the actual number of individuals of the population. Size is the focus of this model because all changes manifest in this quantity. When the population grows, size will increase and when the population declines, size will decrease. The size is given the quantity space {Zero, Low, Medium, High}. Zero population size means the population does not exist. The magnitudes above zero describe the various possible qualitative sizes of the population.

Biomass – The total mass of all individuals in the population is represented in this quantity. This is actually a propagation quantity of size and will change in the same way as size does. Because of this Biomass has the same quantity space as size, {Zero, Low, Medium, High}. When size is zero and the population does not exist, biomass ceases to exist so biomass will never become zero.

Resource_need – Resources needed by a population to sustain itself. The resource need is subtracted from the available resources to calculate the fulfilment rate and thus the quantities resource need and available resources need to be comparable. Furthermore the resource need is calculated by using the biomass of the population and thus these quantity spaces also need to be comparable. Resource need also has the quantity space {Zero, Low, Medium, High}.

Per_capita_birth – The average birth rate per individual. This quantity only needs to positively influence the size and be comparable to death, so a smaller quantity space is sufficient. For capita birth {Zero, Plus} is used. Like Biomass and Resource need, Capita birth can never become zero because it simply ceases to be relevant when the size is zero.

Per_capita_death – The average death rate per individual. Like birth, this quantity can suffice with a small quantity space. For per capita death {Zero, Plus} is used. Like per capita birth, per capita death can never become zero because it ceases to exist when size becomes zero.

Fulfilment_rate – The rate which indicates whether the resource need can be satisfied or not. When the resource need can be satisfied, this rate is positive and when the resource need cannot be satisfied it is negative. For this quantity {Min, Zero, Plus} is used.

Open population quantities

Immigration – When the population is open, individuals of the same species but originally members of another population can move into the initial population. This rate only exists when this is the case. The quantity space is {Zero, Plus}. Zero occurs only when immigration stops to occur. Immigration directly influences the size of the population positively when it is plus.

Emigration – Individuals of the initial population can move out of it to other populations when the population is considered to be open. The quantity space for this rate is also {Zero, Plus}, and becomes zero only when emigration stops to occur. Emigration has a direct negative influence on the population size when it is plus.

Environment quantities

Resource_available – The amount of resources that is available in the environment. The constant rate with which resources replenish in the environment adds to this amount of available resources. It decreases when resources are used by the population. This quantity has the quantity space {Zero, Low, Medium, High}.

Table 4.1: Quantities and quantity spaces as implemented in the modelling task.

Quantity	Quantity space
Size	{Zero, Low, Medium, High}
Biomass	{Zero, Low, Medium, High}
Resource_need	{Zero, Low, Medium, High}
Per_capita_birth	{Zero, Plus}
Per_capita_death	{Zero, Plus}
Fulfilment_rate	{Min, Zero, Plus}
Immigration	{Zero, Plus}
Emigration	{Zero, Plus}
Resource_available	{Zero, Low, Medium, Plus}

4.3.3 Assumptions

Theoretical assumptions

To clarify the standards the model needs to meet and reduce the possible outcomes of the behaviour due to ambiguity, several assumptions about the world, population and environment are made.

- The inflow of resources into the environment is considered to be constant. This means that there will be no disturbances of the environment that will cause the available resources to decline or increase.

The single population model is complex in nature. The following assumptions are used to reduce ambiguity and complexity of the simulation results.

- #### 4.3.4 Model fragments

The single population includes 22 model fragments. To describe them in a logical and comprehensive way, the names from the overview in Figure 4.3 are used. The model fragments are described according to their inclusion into the most important aspects of the model, the environment, the internal population dynamics, the regulatory processes, the usage of resources by the population and the open population.



Modelling the environment

The environment needs an entity *Environment* and introduces the quantity *Resource_available*. The *Environment* model fragment is used as the parent for the other environment related model fragment and shown in Figure 4.4. The *Resource_available* quantity gets a fixed value in the scenario and its derivative is set to zero. This model fragment is called *Assume simple environment*, and is shown in Figure 4.4.

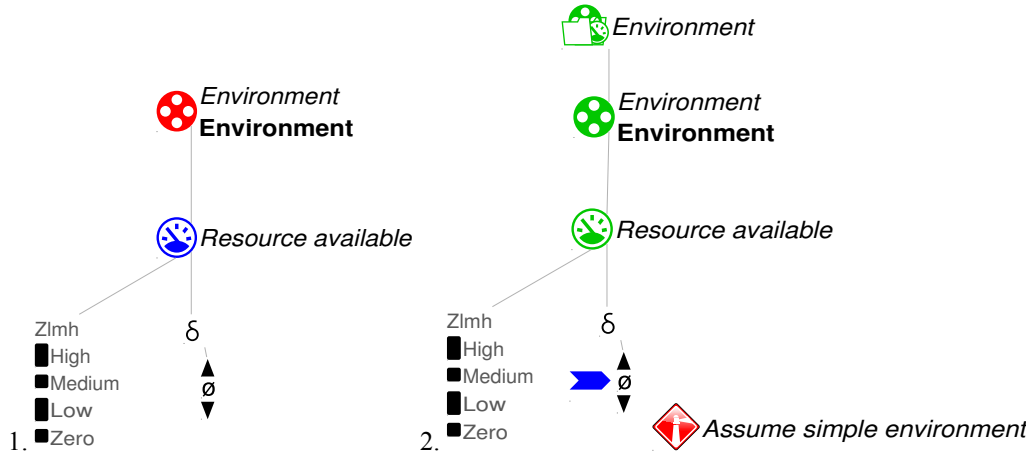


Figure 4.4: 1. The *Environment* model fragment.
 2. The *Assume simple environment* fragment, descended from *Environment*.

Modelling the population dynamics and regulatory processes

A population has several quantities to describe its internal behaviour. To begin with, a population has a *Size* quantity. This quantity is implemented in the *Population* model fragment, as shown in Figure 4.5. From the *Population* model fragment, two other fragments descend, which define the conditions for an existing and a non-existing population. These are also shown in Figure 4.5. A side effect from this modelling choice, which is caused by the simulation preferences (see section 4.4.1), is that when the population *Size* quantity drops to Zero, the elements added in the model fragments which only descend from the existing population, will cease to exist in the model. In effect, a population which goes extinct, cannot begin to grow anew.



Figure 4.5: 1. The *Population* model fragment.
 2. The *Population that exists* model fragment.
 3. The *Population that does not exist* model fragment.

Biomass and Resource_need depend on Size. This means that Biomass and Resource_need react to changes in the same way as Size does and reflect its behaviour. Because they are calculated by a positive proportionality from Size to Biomass and then propagate further to Resource_need, the quantities are all implemented in their own model fragment. In Figure 4.6, the model fragment *With resource need* is shown, which also shows how Biomass is propagated from the changes in Size.

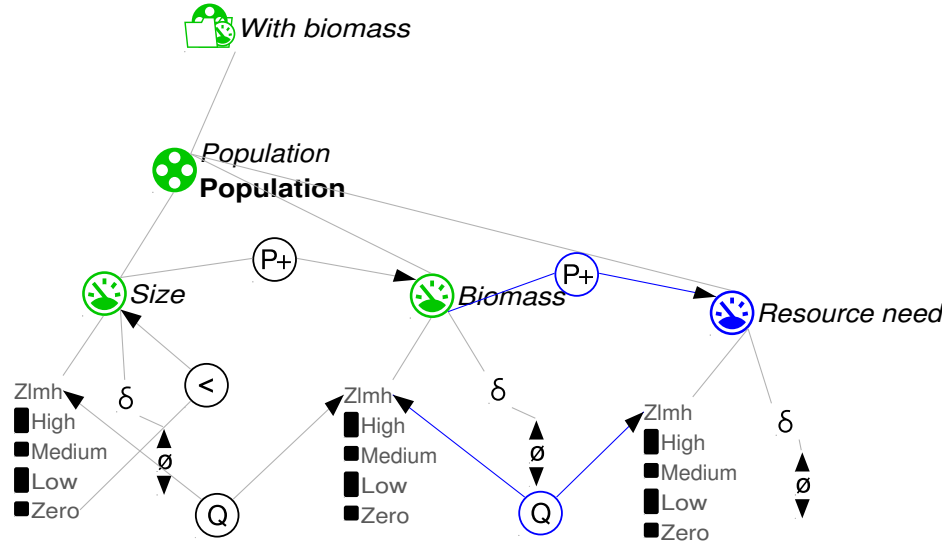


Figure 4.6: Static *With resource need* model fragment.

The Per_capita_birth and Per_capita_death quantities are added later as process model fragments, like shown in Figure 4.7. They describe the rates of the birth and death processes. There is a positive influence from per Per_capita_birth to Size and a negative influence from Per_capita_death to Size. This means that Per_capita_birth adds to the population size and Per_capita_death subtracts from it, effectively adding the outcome of both quantities in the Size quantity. To calculate the outcome of adding these influences together in Size, their relative force must be known. To this end the *Inequalities birth and death* model fragment and its descendents are implemented (see Appendix C).

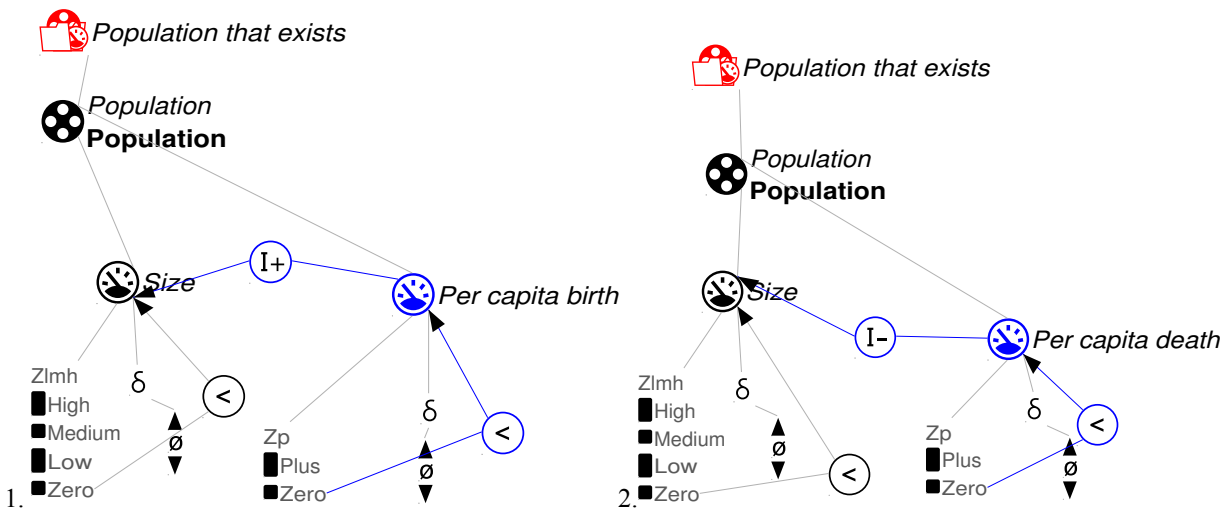


Figure 4.7: 1. The *Birth* process model fragment.
2. The *Death* process model fragment.

Fulfilment_rate describes if and how much the resource need of the population is fulfilled. It has been a point of argument whether this quantity should be part of the environment or be attached to the population itself. But because almost every population has a different diet, it is not possible to capture whether or not its needs are fulfilled in one single quantity when dealing with multiple populations.

The value of Fulfilment_rate is calculated by subtracting the Resource_need of a population from the Resource_available in the environment. Its derivative is calculated by adding a positive proportionality from Resource_available and a negative proportionality from Resource_need. Fulfilment_rate is added to the model in the *Complete population* model fragment, and given its value in the *Production* model fragment shown in Figure 4.8. To calculate the outcome of the Min relation between Resource_need and Resource_available correctly, the *Inequalities resource need and available resources* are added to the model. Like the *Inequalities birth and death*, these model fragments force the reasoning engine to test all possibilities consistently. This model fragments are also shown in Appendix C.

The Fulfilment_rate quantity indicates whether there are enough resources for the population or if there is resource shortage. When there is resource shortage the Fulfilment_rate is Min. Per_capita_death should increase and Per_capita_birth should decrease. But when there are enough resources to fulfil the need of the population, Per_capita_birth should increase and Per_capita_death will decrease. This is modelled by creating a positive influence from Fulfilment_rate to Per_capita_birth and a negative influence from Fulfilment_rate to Per_capita_death. When Fulfilment_rate is Plus, which means there are enough resources, the influence on Per_capita_death will be negative and the influence on Per_capita_birth will be positive. However, when Fulfilment_rate is min, a negative influence will have positive output and a positive influence will become negative, making Per_capita_death increase and Per_capita_birth decrease.

The change from growth towards decline of the population is not immediate when resources are scarce. It may take some time before deaths exceed births and the population actually begins declining.

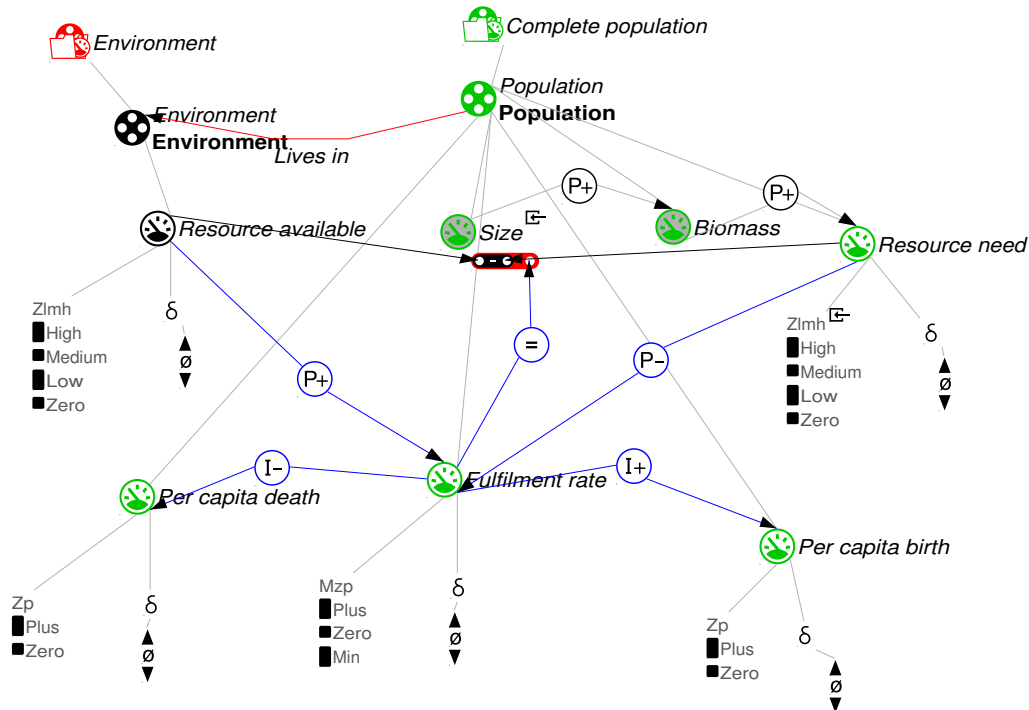


Figure 4.8: The *Production* process model fragment.

To make calculations less ambiguous for the reasoning engine, an assumption is added as a model fragment, as shown in Figure 4.9. The assumption labelled 'Assume equality between needed and available resources' can be added to a scenario to activate this model fragment. The equality statement between the quantities Resource_available and Resource_need makes their quantity spaces comparable,

which means that Medium value in Resource_available is of equal magnitude as Medium value in Resource_need.

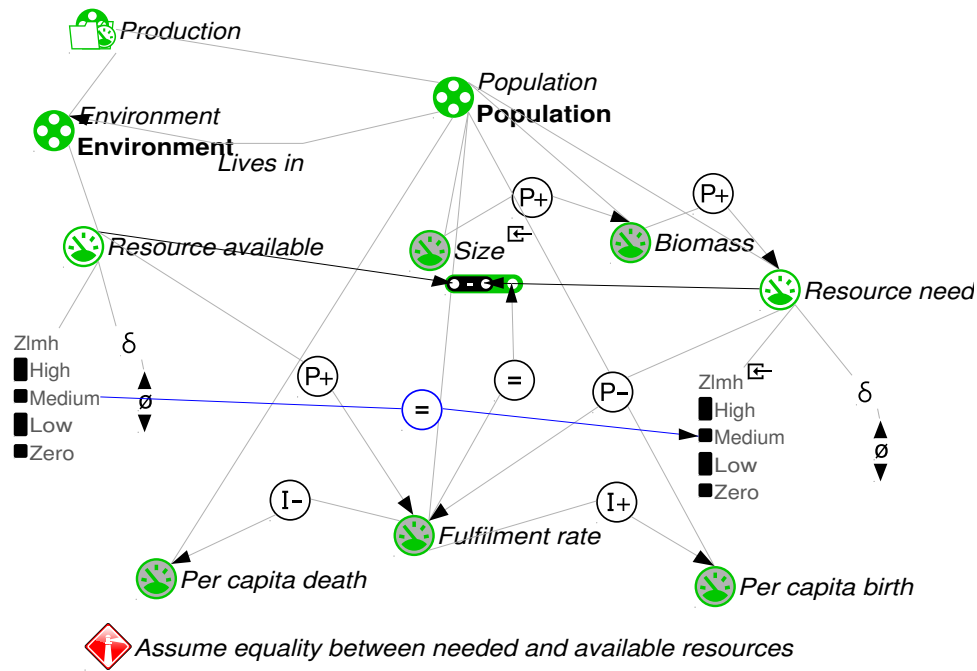


Figure 4.9: The *Assume equality between needed and available resources* model fragment.

Modelling the open population

The literature (Campbell & Reece, 2002) mentions immigration and emigration as the only other two processes that can affect population size. They are modelled in the same way as the birth and death processes, having a positive and a negative influence on Size respectively. Since they are quantities of the population, they are already attached to the population in the static model fragment *Assume open population*, as a child of the original population fragment. An assumption determines whether the population is open or closed. A closed population has no external influences which excludes immigration and emigration from the model. An open population can be influenced by external factors and thus immigration and emigration are added to the population when it is assumed to be open like shown in Figure 4.10.

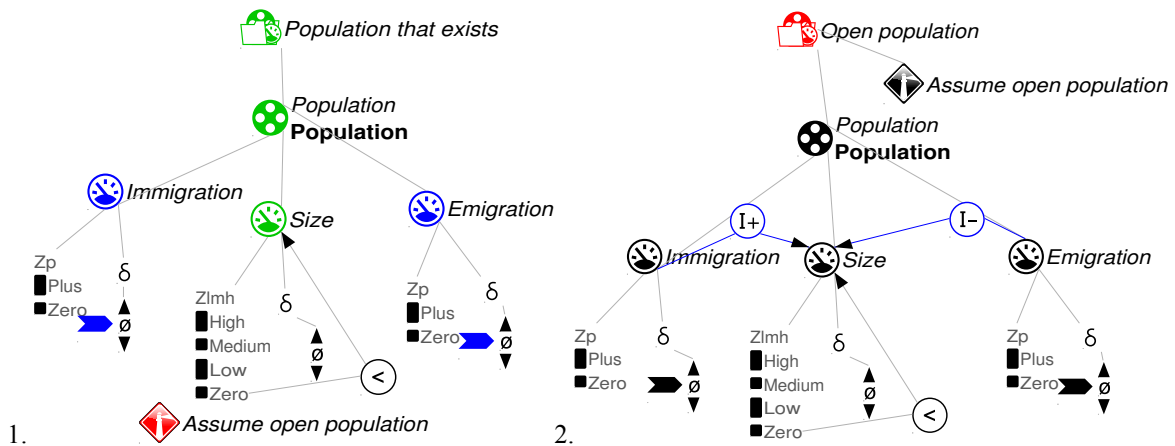


Figure 4.10: 1. The *Assume open population* model fragment.
2. The *Immigration and emigration* process fragment.

4.4 Simulation

For the single population several scenarios were created. The results of simulations ran on these scenarios are made visible by Garp3 in state-graphs of connected nodes, like explained in chapter 2. The states of the state-graph that results from simulation of the scenarios are investigated one by one to see how and why the quantities change from one state to another. Paths of possible behaviour are identified and compared with the predictions in section 4.2.4. Possible end- and initial states are inspected to get a better insight into the mechanisms implemented in the model fragment library. Also, the dependencies of several typical states in the state-graph are shown to evaluate if the model fragments library is properly implemented.

4.4.1 Simulation preferences

In the simulations of the single populations the simulation preference ‘remove inactive quantities’ is used to make it possible for the population to reach extinction (see Chapter 2).

When the size of the population is zero and there are no individuals left in the population, biomass, size, and the birth- and death rates are also zero. Modelling this can cause some problems however, because birth and death rates are averages and will thus increase when the population declines in size. In qualitative values it is not possible for a quantity to go from its maximum value directly towards zero, thus the actual quantitative process can never be modelled. That is why the choice is made to delete the quantities that also become zero from the structural model in the reasoning engine, when the population size reaches zero.

4.4.2 Scenario 1: Growing population

The Growing population scenario serves to investigate if the model fragments concerning the population are correct. This is a simple scenario, shown in Figure 4.11, and its purpose is to test the population dynamics implemented in the model.

In this scenario *Per_capita_birth* and *Per_capita_death* are given a value and *Size* is set to Low to make the population exist. When equality conditions between *Per_capita_death* and *Per_capita_birth* would also be supplied initially, only growth or decline of the population will occur in the simulation. Without such additional information the simulation the simulator will try all possibilities.

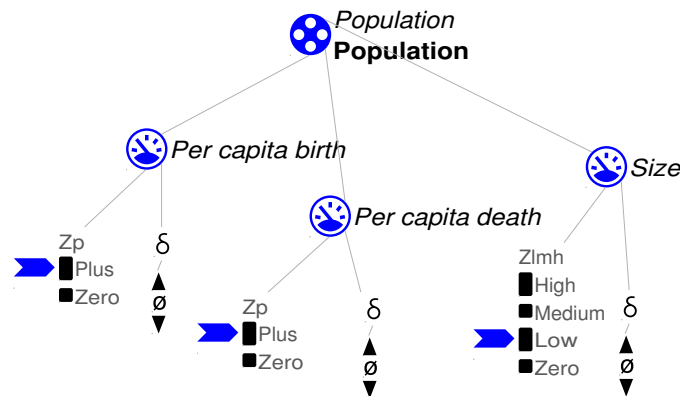


Figure 4.11: Scenario 1 of the Single population model.

Initial states

When the simulation starts, it shows three initial states in the state-graph, as shown in Figure 4.12. These three states represent the three possible behaviours the population can show from the initial scenario in which *Size* is set to Low. Births can be higher than deaths, causing growth of the population, or births can be lower than deaths, causing decline of the population *Size* and eventually extinction of the population, or both rates could be equal, resulting in stabilization. There are no influences on *Per_capita_birth* and

Per_capita_death in this scenario, which means that these quantities will not change during the simulation.

Behavioural paths

When looking at the fully simulated state-graph in Figure 4.12, three paths, each resulting from one of the three initial states, can be seen.

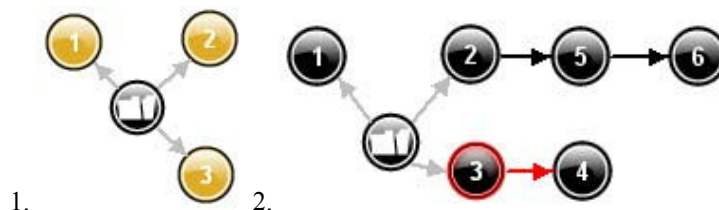


Figure 4.12: 1. The initial states of the simulation of scenario1.
2. The whole state-graph of the *Growing population* simulation.

In Figure 4.X, the value histories for these three paths are shown. The first path, which consists of only state 1, shows the static population where Per_capita_death and Per_capita_birth are equal to each other. Path 2, consisting of states 2, 5 and 6, shows the growing population, where births are higher than deaths and the population increases. Path 3, which consists of state 3 and 4, shows decline and eventual extinction of the population, as a result of Per_capita_death being higher than Per_capita_birth.

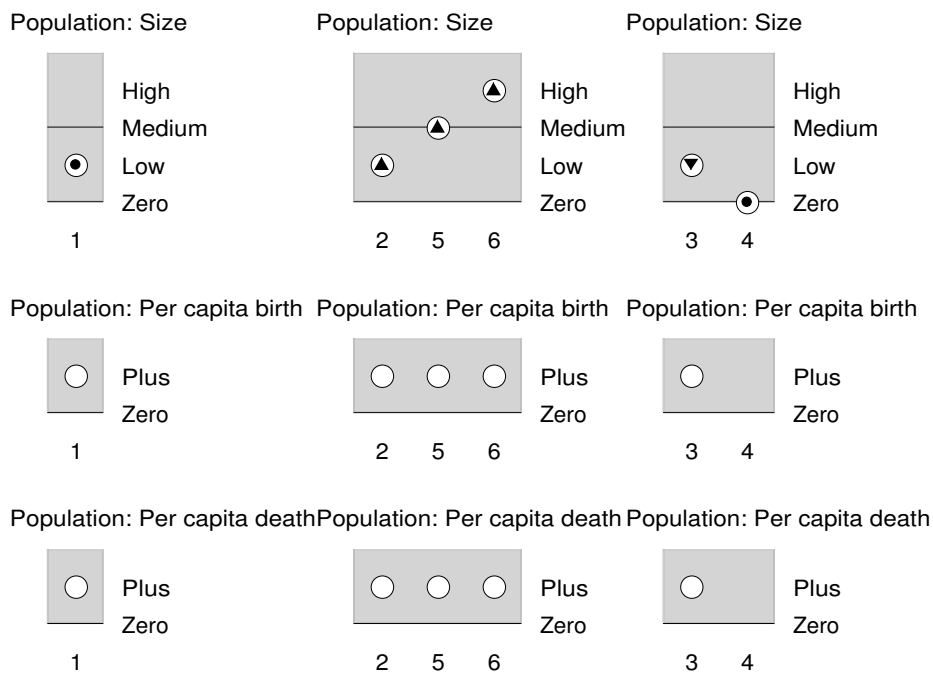


Figure 4.13: Value histories for paths 1. {1}, 2. {2,5,6} and 3. {3,4}.

In the equation history the changes in equality relations can be investigated. To whether the different paths are actually the result of the equality relation between Per_capita_death and Per_capita_birth, the equation history is shown in Figure 4.X. State 4 cannot be shown in the equation history because the quantities Per_capita_death and Per_capita_birth are removed from the system structure by the reasoning engine when the population goes extinct in state 4.

Per capita death (Population) ? Per capita birth (Population)

> = < < <

3 1 2 5 6

Figure 4.14: Equation history for all states, except state 4.

End states

Scenario 2 has three end states, 1, 4 and 6. State 1 shows an equilibrium from which no other behaviour can be derived. State 4 shows a population that has grown towards its maximum. The quantity space allows no more transitions from High and thus the path ends. State 6 shows a population that has gone extinct. When a population goes extinct, all quantities except for Size are deleted from the system structure by the reasoning engine. From the state of extinction no further changes are possible for the population, thus the path ends.

Causal model

More details about the simulation can be gained from investigation of the dependencies. Except for state 4, all states show the same set of dependencies as shown in Figure 4.15, but with a different equality relation as shown in the Figure. The figure also shows the dependencies for the extinction of the population in state 4, which includes only the quantity Size, which is also illustrated in Figure 4.15. The causal model is thus derived correctly from the model fragment library and it is safe to assume that the implemented causality within the population is correct. Because the simulation lacks an environment, the Fulfilment_rate quantity has not received a value in this simulation and is thus not connected through causality with the other quantities in the population.

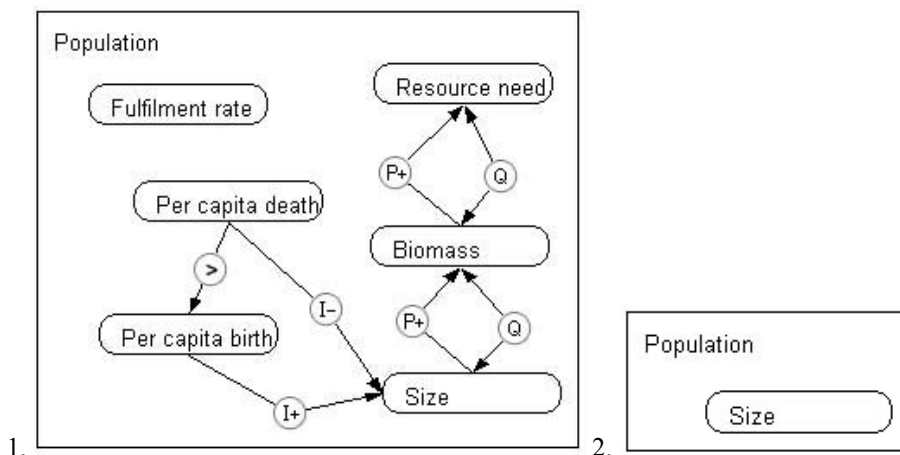


Figure 4.15 1. Dependencies in state 3 .
2. Dependencies in state 4.

4.4.3 Scenario 2: Population in a simple environment

The population with the 'simple environment' assumption, implements a population growing on the environment with a static threshold which cannot change. As shown in Figure 4.16, it implements the whole system structure defined in section 4.2.

The population is connected through a *lives in* configuration to the environment and grows under influence of the available resources. There are several possible variations to the initial conditions to adapt the scenario. Equalities between Per_capita_birth and Per_capita_death can distinguish between an initially growing and an initially declining population. Equalities between Resource_available of the environment and Resource_need of the population can distinguish between initial resource shortage and abundance. These equalities are not necessary to run the simulation however. Without them the simulation gives all possible behaviours.

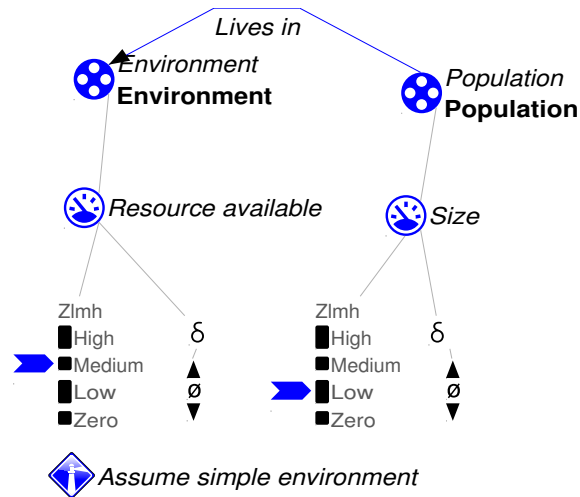
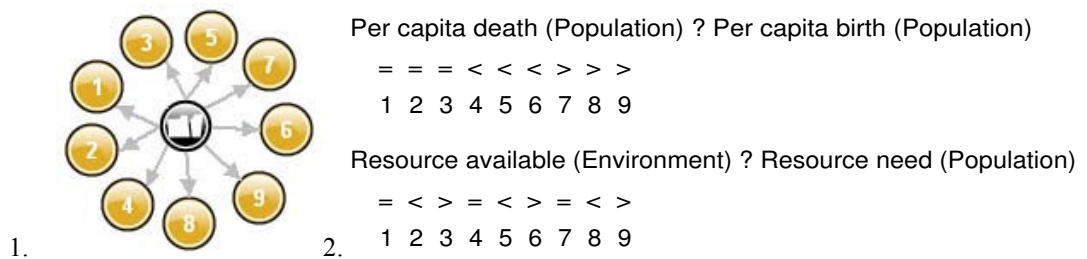


Figure 4.16: Scenario 2 of the Single population model.

Initial states

When the simulation is started, it generates nine initial states, as shown in Figure 4.17.

Figure 4.17: 1. The initial states 1,2,3,4,5,6,7,8,9 of scenario 2.
2. The equation history for the initial states of the simulation.

In the equation history, also shown in Figure 4.17, part of the explanation for these initial conditions can be found. The other part is found in the value history, shown in Figure 4.18.



Figure 4.18: The value history for the initial states.

The reasoning engine will try all possibilities which it can derive from the model fragment library. From the initial value of Low that the Size quantity gets at the beginning, it can begin to increase, stabilize or decrease. In Figure 4.18 it is clear that all options are tried. Then, the Fulfilment_rate will be calculated

by subtracting the Resource_need from the Resource_available. Because the equality relation between Resource_need and Resource_available can be greater than, equal to or smaller than, for each possible derivative of Size, all three possible equalities are tried. Fulfilment_rate determines how the Per_capita_birth and Per_capita_death rates are going to change, and because there are nine possibilities for Fulfilment_rate in total, nine values for births and deaths are calculated.

Behavioural paths

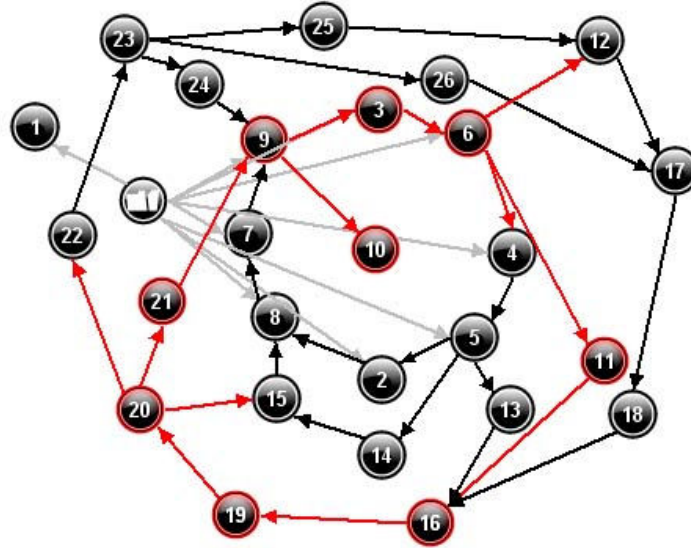


Figure 4.19: The complete state-graph of scenario 2 with selected cyclic path {9,3,6,11,16,18,19,20,21,9} and the ending path {9,3,6,11,16,18,19,20,21,9,10}.

To investigate the behaviour, paths can be selected and the transitions between quantities and equalities can be analysed. First a path is selected like shown in Figure 4.19. Paths begin with one of the initial states, which are defined by the grey arrows. The path {9,3,6,11,16,18,19,20,21,9} is cyclic, which means that the behaviour it represents can repeat itself endlessly. However, the same path can also end when it follows {9,3,6,11,16,18,19,20,21,9,10}. State 10 is an end state, a state that represents a possible ending to the behaviour in the simulation.

The state-graph shows that there are more possible paths of behaviour to follow than the one selected. From the nine initial states, state 1 becomes an end state and the rest of the initial states form a cyclic path at the centre of the state-graph. From this cyclic path at the centre, several links to cyclic paths around the centre are made, so that the state-graph becomes a connected graph of intertwining and crossing circles. A path of behaviour could begin in one of the inner circles and then repeat itself in one of the outer circles and then shift to the inside again. The different circles represent possible fluctuations in the quantity spaces of Size, Biomass and Resource_need.

The selected states only show two possible paths, but reveal nothing about the values of the states or what happens in the transactions between the states, which describe the actual behaviour. To investigate what happens in the selected paths the value history can be inspected as shown below in Figure 4.20.

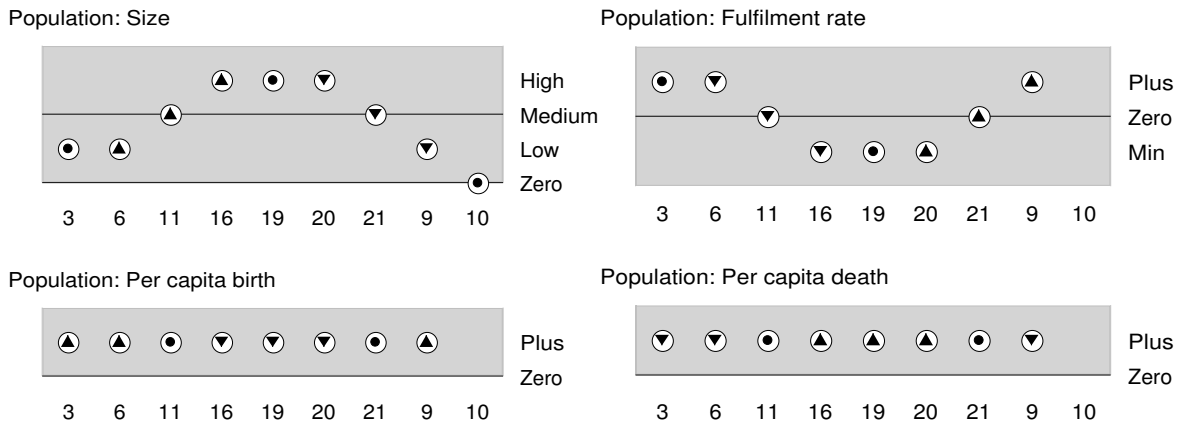


Figure 4.20: The value history for the selected paths.

It must be kept in mind when reading this value history that the cyclic path does not end in state 9, but goes back to state 3 to continue its behaviour. There is also a path directly from 9 to 10. When the path starts in state 3, the population Size begins stable in Low and then starts to increase. While Fulfilment_rate is Plus, the Per_capita_birth rate increases and Per_capita_death rate decreases, making births higher than deaths. In state 11, the Fulfilment_rate becomes Zero, stabilizing the birth- and death rates, but as shown in the equation history in Figure 4.21, keeping the birth- and death rates unequal.

Per capita death (Population) ? Per capita birth (Population)

= < < < = > > >
3 6 11 16 19 20 21 9

Resource available (Environment) ? Resource need (Population)

> > = < < < = >
3 6 11 16 19 20 21 9

Size (Population) ? Zero

> > > > > > > =
3 6 11 16 19 20 21 9 10

Figure 4.21: The equation histories for the selected paths.

When Fulfilment_rate drops below Zero because the population gets too big to be supported by the environment, Per_capita_birth decreases and Per_capita_death increases. It takes a while before the death rate exceeds the birth rate and the population starts to decline in size. In state 19, the Size quantity stabilizes because the birth- and death rate become equal, and in state 20, it begins to decrease. Then, when the population has become small enough to be supported by the environment again, the path of states splits. It can go to state 3, in which the population begins increasing anew in the cycle from state 3 to state 9. But it can also happen that the population goes extinct because it does not recover fast enough from the setback by starvation. Then the path goes towards state 10, and ends there.

The behaviour that is shown is an accurate reflection of what was predicted in section 4.2. Although extinction seemed unlikely, it is a logical explanation that it could happen that the population does not recover fast enough from starvation and goes extinct.

End states in the state-graph

As illustrated in Figure 4.19, there are two end-states in the state-graph of the single population, states 1 and 10. As can be seen in Figure 4.20, state 10 represents the extinction of the population by starvation.

As explained in the previous section, the reasoning engine tries all possibilities and when calculating the path from state 9 to 3, it does find a possibility that the Size quantity will go towards zero. As explained in the modelling choices, the other quantities disappear from the causal model in the reasoning engine when the size of the population reaches zero. The other end state in the state-graph is state 1. Figure 4.22 shows the quantity values of state 1. This state represents the total stabilization of the population. Because the Per_capita_birth and Per_capita_death rates are equal to each other and the Resource_available and Resource_need are also equal to each other, nothing changes in the population. It is in equilibrium.

	Biomass (Population):	Low, 0			
	Fulfilment rate (Population):	Zero, 0			
	Per capita birth (Population):	Plus, 0			
	Per capita death (Population):	Plus, 0			
	Resource available (Environment):	Low, 0			
	Resource need (Population):	Low, 0	Resource available (Environment):	Low, 0	
1.	Size (Population):	Low, 0	2.	Size (Population):	Zero, 0

Figure 4.22: Quantity values in state 1 and state 10.

The causal model

Figure 4.23 shows the dependencies in a state of the state-graph of this scenario. It seems to correspond to the causal model that was constructed earlier in this chapter. The causal model of State 10 is shown in 4.24, and shows that all other quantities in the extinct population are deleted by the reasoning engine when Size reached Zero.

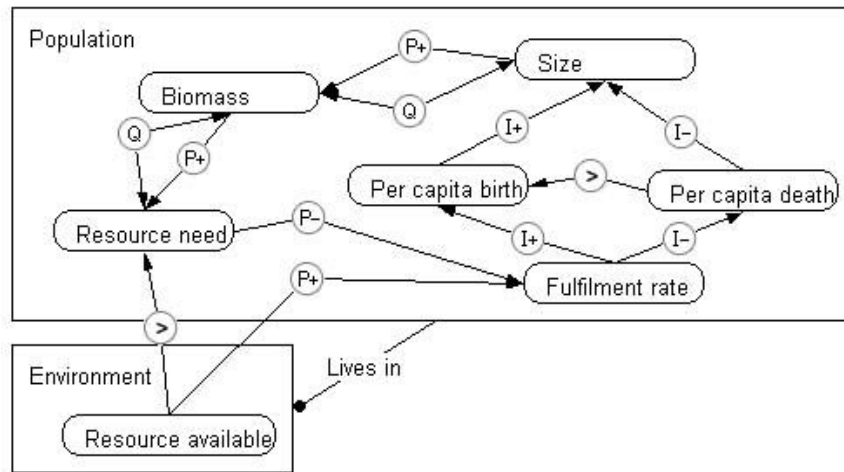


Figure 4.23: Dependencies in state 21 of scenario 2.

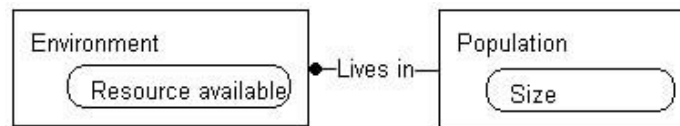


Figure 4.24: Dependencies in state 10 of scenario 2.

4.4.4 Scenario 3: Population in simple environment with equality

The *Population in simple environment with equality*, shown in Figure 4.25, is an extension of the *Population in simple environment*. The assumption ‘Assume equality between needed and available resources’ is added, which allows the addition of one additional model fragment in the reasoning engine when this scenario is selected for simulation which implements an additional equality between

Resource_available and Resource_need. This reduces ambiguity caused by uncertainty about the equality relation between these quantities, which effectively reduces the amount of possibilities the reasoning engine needs to try.

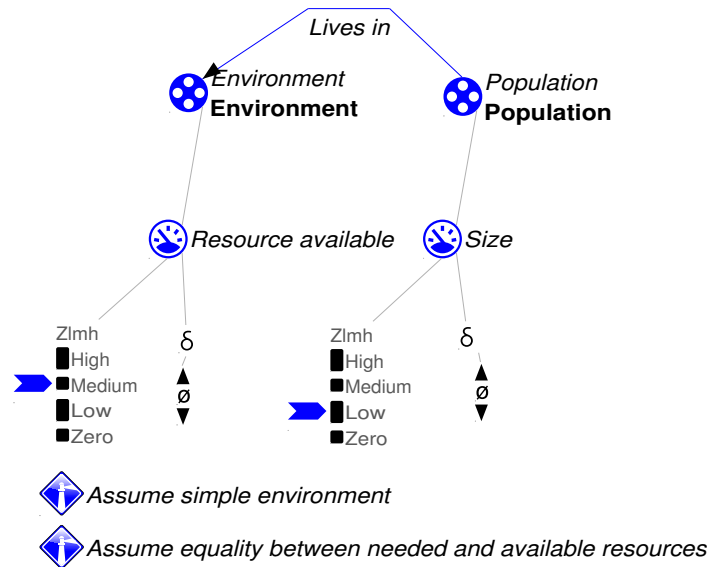


Figure 4.25: Scenario 3 of the Single population model.

Initial states

When the simulation is started, the state-graph shows three initial states, which is a reduction of 6 states compared to the Population in simple environment simulation. The initial states are shown in Figure 4.26, which also shows the equation history. Since it is defined by the added assumption that Medium Resource_available is bigger than Low Size (which equals Resource_need), the reasoning engine only has to try the greater than relation, as shown in the equation history of Figure 4.26. For the equality relation between Per_capita_death and Per_capita_birth, all possible equalities are tried.

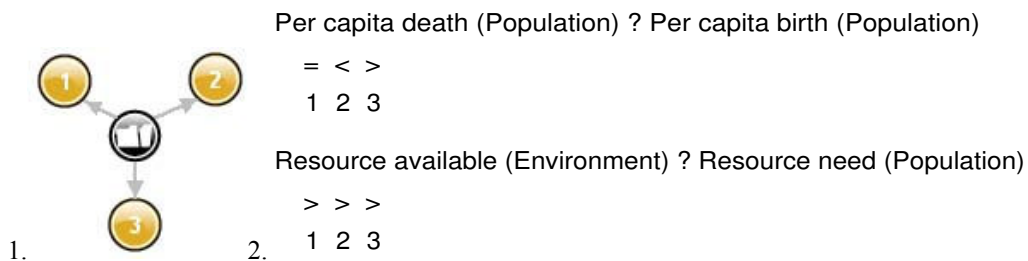


Figure 4.26: 1. The initial states and 1,2 and 3 of scenario 3.
2. The equation history of the initial states.

The different equalities between Per_capita_birth and Per_capita_death, result in three possibilities for the derivative of Size and Fulfilment_rate to begin simulation with, as shown in the value history in Figure 4.27. Since Resource_available is greater than Resource_need for all initial states, the magnitude of Fulfilment_rate is Plus, Per_capita_birth is increasing and Per_capita_death is decreasing for all three states.

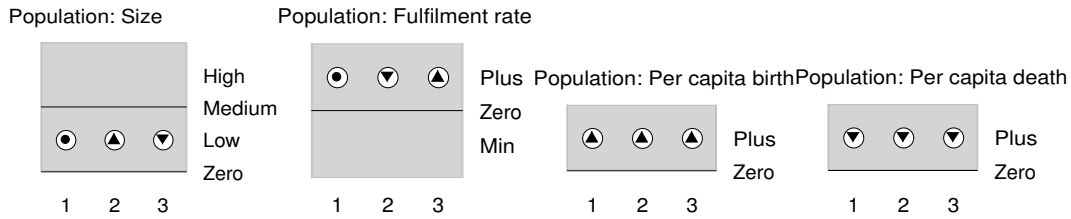


Figure 4.27: The value history for initial states 1, 2 and 3.

Behavioural paths

The complete state-graph of the *Population in simple environment with equality* is shown in Figure 4.28. There are only two complete paths which can be selected. The cyclic path is $\{1, 2, 5, 6, 7, 8, 9, 3, 1\}$ and the ending path is $\{1, 2, 5, 6, 7, 8, 9, 3, 4\}$, as selected in the figure.

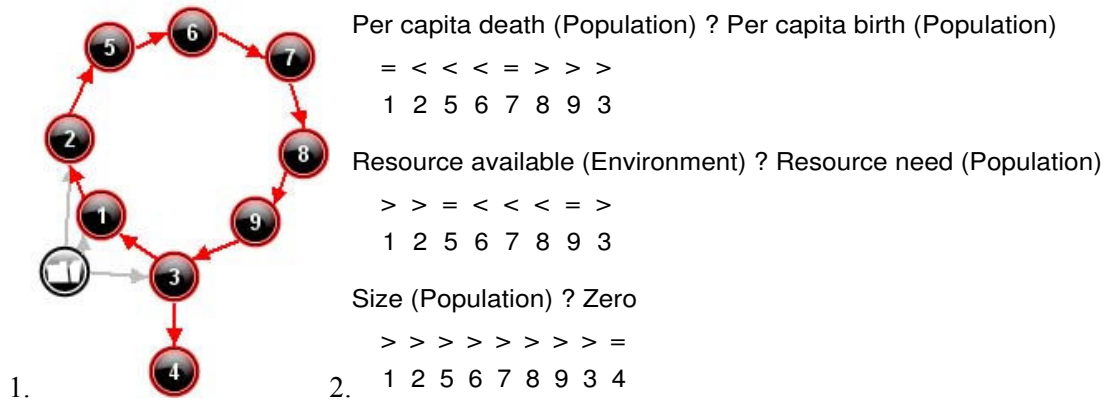


Figure 4.28: 1. The complete state-graph of scenario 3 with selected cyclic path $\{1, 2, 5, 6, 7, 8, 9, 3, 1\}$ and the ending path $\{1, 2, 5, 6, 7, 8, 9, 3, 4\}$.
2. The equation history for the selected paths.

The value histories of the important quantities in the simulation are shown in Figure 4.29. Although the states are numbered differently, the value history is equal to the value history of the paths selected in the *Population in simple environment model*. The equation history, shown in Figure 4.28 together with the state-graph, is also equal to the equation history of the simulation in the previous section.

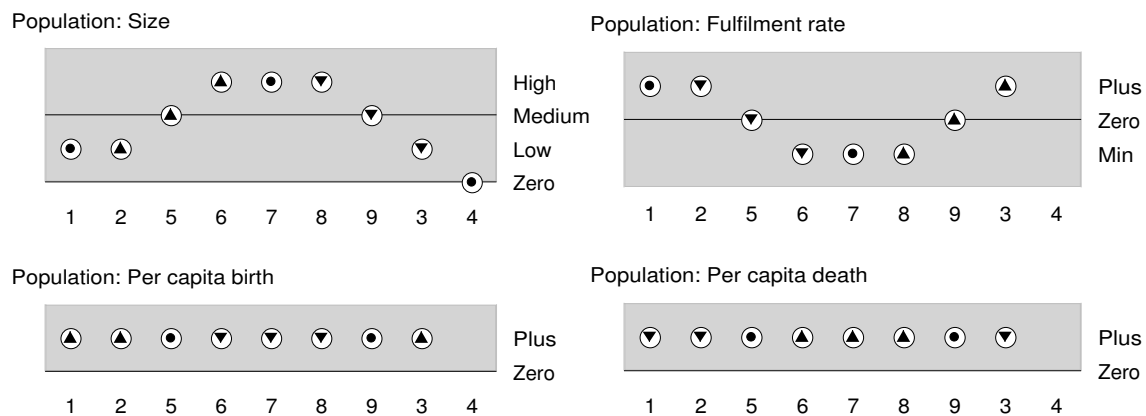


Figure 4.29: The value history for the selected paths.

With a small adaptation, the behaviour is as follows: The path starts in state 1, in which the population Size begins stable in Low and then starts to increase. While Fulfilment_rate is Plus, the Per_capita_birth

rate increases and Per_capita_death rate decreases, resulting in births exceeding deaths. In state 5, the Fulfilment_rate becomes equal to Zero, stabilizing the birth- and death rates, but as shown in Figure 4.28, keeping the birth- and death rates unequal. When Fulfilment_rate drops below Zero because the population gets too big to be supported by the environment, Per_capita_birth begins to decrease and Per_capita_death begins to increase. It takes a while before the death rate exceeds the birth rate and the population starts to decline in Size. In state 7, the Size quantity stabilizes because the birth- and death rate become equal, and in state 8, it begins to decrease. Then, when the population has become smaller again, the path of states splits. It can go to state 1, stabilizing the Size quantity, so the population begins increasing anew in the cycle from state 1 to state 3. But it can also happen that the population goes extinct because it does not recover fast enough from the setback by starvation. Then the path goes towards state 4, and ends there.

The behaviour in this scenario is a lot less ambiguous than the behaviour in scenario 2 and this behaviour is also an accurate reflection of what was predicted in section 4.2. Again the simulation shows extinction, which is logical when explained by inspection of the state-graph.

End states

Where the previous simulation without the added assumption has two end states, this simulation has only one end state. Because the assumption reduces the amount of possible transitions from the initial scenario, the stable state from scenario 2 can never follow from the initial conditions in this scenario. In Figure 4.28 and 4.29 it can be found that the only end state in this scenario is the extinction state 4. Like in scenario 4, the end state in which the population goes extinct loses all quantities except for Resource_available in the environment and Size of the population. The magnitude of Size goes to Zero and the behavioural path ends.

The causal model

Figure 4.23, in the previous section, shows the causal model or dependencies in state 1,2,3,5,6,7,8 and 9. The end state 3 dependencies are equal to those shown in 4.24, in the previous section. The causal models correspond to the constructed model in section 4.2.

4.4.4 Scenario 4: Open population in simple environment with equality

Immigration and emigration are mentioned as external influences on the population and potentially important processes next to the processes of birth and death. The assumption ‘Assume open population’ is used to include the possible influences of Immigration and Emigration. As initial conditions the equality between both external influences can be varied, but both quantities must be given a magnitude value in the scenario itself. The scenario is shown in Figure 4.30.

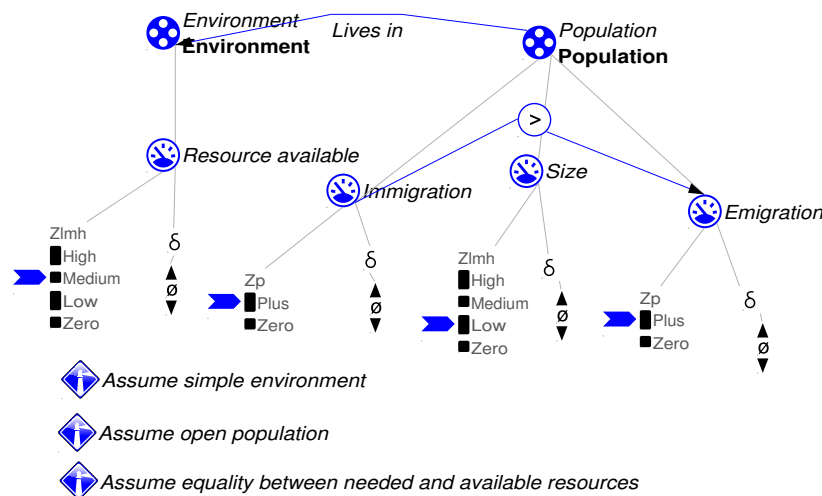


Figure 4.30: Scenario 4 of the Single population.

Initial states

When the simulation is started, the reasoning engine finds 5 initial states, shown in Figure 4.31. When looking at the equation history, which is also presented in Figure 4.31, it shows that only the equality relation between *Per_capita_death* and *Per_capita_birth* shows several possibilities. This inequality can be equal, lesser than or greater than. But when the deaths exceed the births, there are three possible paths the simulation can follow.

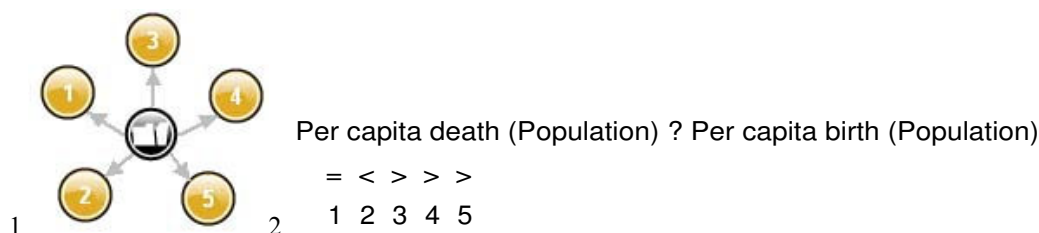


Figure 4.31: 1. The initial states of scenario 4.

2. The equation history of the initial states.

When looking at Figure 4.32, which shows the value history of the initial states, it is evident that when deaths exceed births, the derivative of *Fulfilment_rate* causes the uncertainty of how the *Size* will change. However, this uncertainty is not caused by changes in the equality relations between *Resource_available* and *Resource_need*, the *Fulfilment_rate* is Plus in all five initial states.



Figure 4.32: The value history of the initial states.

The three possible changes in the derivative of *Fulfilment_rate* are caused by the uncertainty whether the growth that occurs by the immigration exceeding emigration, exceeds the decline caused by deaths exceeding births at the beginning. The three possible derivatives of *Size* are propagated to *Resource_need* and then to *Fulfilment_rate*, which causes the behaviour observed in Figure 4.32.

Behavioural paths

The complete state-graph of scenario 4 is presented in Figure 4.33.

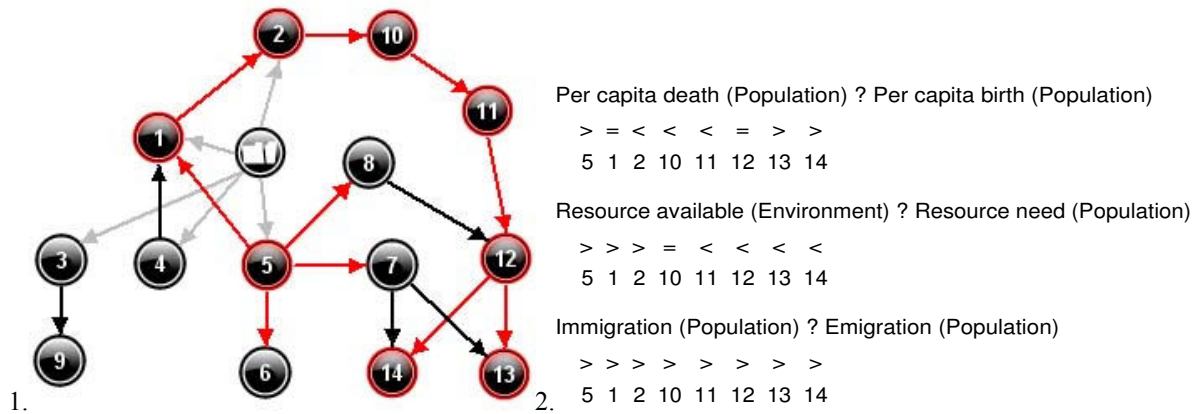


Figure 4.33: 1. The complete state-graph of scenario 4 with selected paths: $\{5,1,2,10,11,12,13\}$ and $\{5,1,2,10,11,12,14\}$.
2. The equation history of both selected paths.

State 13 and 14 represent the end states of the population where it has reached its maximum value because Immigration exceeds Emigration. For both these end states, 3 paths can be distinguished starting from state 5, and one path from state 4. Also, there is one separate path to end state 9, and from state 5 end state 6 can be reached. To analyse the behaviour which is represented in the selected paths, the value history of these paths is shown in Figure 4.34.

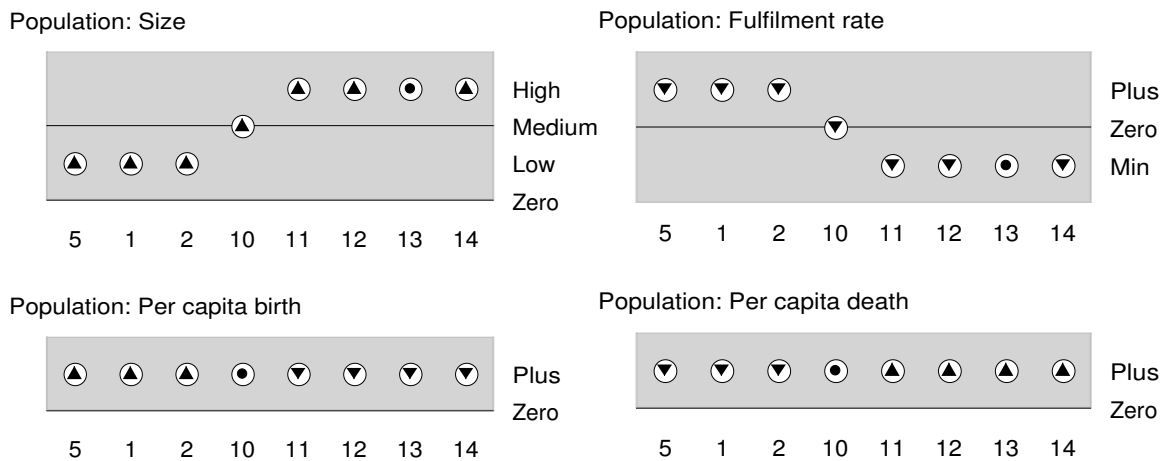


Figure 4.34: The value history of the selected paths.

When looking at the value history, it becomes clear that despite the value of the Fulfilment_rate, the population keeps growing. After state 10, the Fulfilment_rate shows that there is not enough food for the population, and Per_capita_death begins to increase. After state 12, deaths exceed births, which can result in stabilization of the population Size and thus its growth, which means that deaths are equal to the individuals that immigrate into the population. Or the population stays growing, which means that the number of individuals moving into the population exceeds the number that dies of starvation.

Although this simulation shows some ambiguity, like the two end states 13 and 14, the behaviour it exhibits is logical and can be explained by the theory. A point of criticism is that a population that stays growing because of immigration but lacks the resources to sustain itself is not likely to occur in nature, because emigration will not remain constant when there is a negative feedback on the population. But this is not captured in the model fragments because this is outside the focus of the modelling task.

End states

The complete state-graph of scenario 4 has four end states. Two have already been described in the previous section as the stabilizing population and the ever expanding population. The quantity values of state 6 are shown in Figure 4.35. A similar state was encountered when looking at the complete simulation of scenario 2. It describes the population at an equilibrium where the number of deaths that exceed births is equal to the number of immigrating individuals that exceed the number of emigrating individuals.

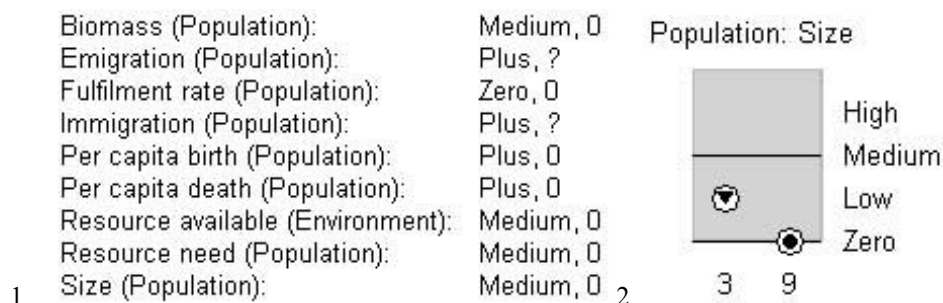


Figure 4.35: 1. The quantity values in state 6.
2. The value history for the Size quantity for path {3, 9}.

The value history for the behaviour path {3, 9} is also shown in Figure 4.35. State 9 is an end state in which the Size quantity is Zero. This can be explained by analysing the equality relation between Per_capita_birth and Per_capita_death in this state in which Per_capita_death exceeds Per_capita_birth. The path {3, 9} represents the possibility where deaths exceed births and even immigration which exceeds emigration can not offset this and the population goes extinct.

The causal model

The dependencies in all states, excluding state 9 where Size is Zero, are presented in Figure 4.36. Like planned in the causal model shown in Figure 4.1, Immigration and Emigration are added to the model and have a positive and negative influence on Size respectively. There is also an equality relation between Emigration and Immigration. The rest of the dependencies is equal to the dependencies in scenario 2 and 3. State 9 has the same dependencies as the states in which Size is Zero from scenario 2 and 3.

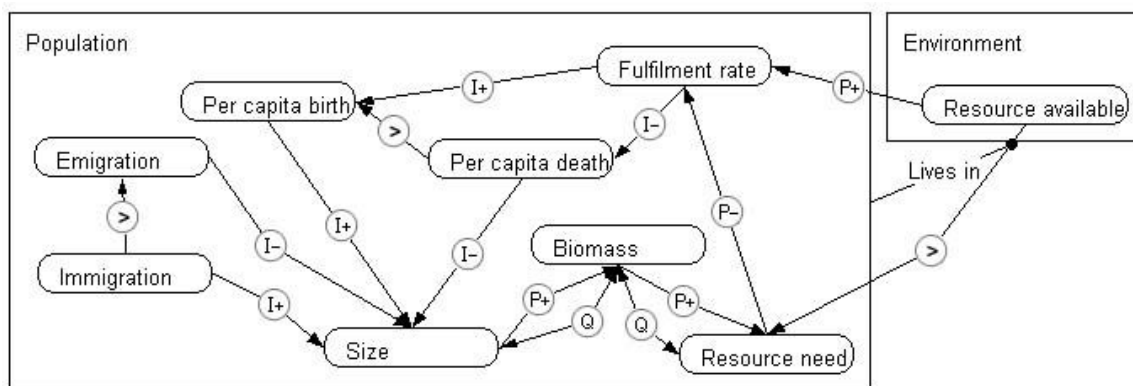


Figure 4.36: The dependencies in state 5 of scenario 4.

4.5 Summary

In this chapter, the knowledge gained about the behaviour of a single population in an environment is analysed and captured in a qualitative model. The model is described and explained in detail. To test the

implemented model, several scenarios have been created which allow simulations of specific situations in which different versions of a single population are involved.

The behaviour of the simulations of the single population qualitative model matches the predictions made from analysis of the theory.

5. Another approach to modelling the single population

5.1 Introduction

The R-star model (Nuttle et al., 2006). is developed in the same period as the Single population, presented in the previous chapter. It was developed for the purpose of exploring the possibility to capture uncertainty in qualitative models, but it implements similar principles as the single population model: A plant population using resources from the environment to sustain itself and grow.

The R-star model implements a plant population growing in an environment. The plant population grows and uses resources from the environment. Because there are plenty resources, the birth rate or capita production rate of the population is increasing. With increasing birth rate, the size of the population also increases. Because there are no external influences on the model, it assumes a constant death rate. The amount of resources available in the environment will decrease when the population size increases and thus consumes more of the resources. This will also cause the production of the population, which is totally dependent on the resources which are available, to decrease. The stable death rate will exceed the lower birth rate, and the population size will begin decreasing. The decrease of the population size will lower the amount of resources it needs, allowing the available resources in the environment to increase again. The production of the population will then rise again because enough resources are available and the population will start growing again.

The description of the system is similar to the single population of previous chapter, but has two important differences. The R-star model assumes a constant death rate which is not influenced by the varying amounts of available resources in the environment. Furthermore, the R-star model assumes that the production or birth rate of the population rises and falls with the available resources in the environment.

5.1.1 Structural details

Entities

The R-star model implements the same entities as the single population model, the population and the environment. Although in the implemented scenarios the population is identified as a plant and more specific; a tree population and the environment as a forest, the R-star model is also generic in nature. Figure 5.1 shows the entities defined in the subtype hierarchy of the R-star model.

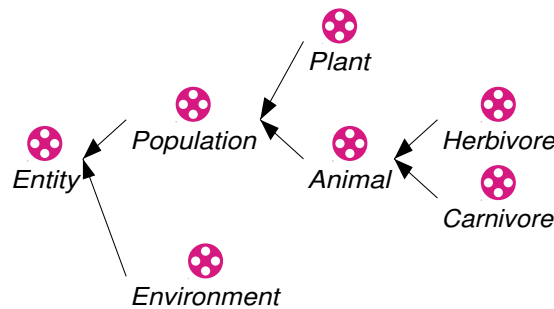


Figure 5.1: The R-star entity subtype hierarchy.

Structural relations

The model implements *Lives in* as a configuration. This has the same meaning as the configuration with the same name which was implemented in the single population model. With this configuration a population can be identified as living in an environment or the tree living in the forest.

5.1.2 Quantities and quantity spaces

An overview of the quantities and quantity spaces of the R-star model is given in table 5.1.

Population quantities

Biomass – This quantity represents the size of the population by adding together the total weight of all the living individuals in it. Compared to the single population, this quantity is equal to the Size, Biomass and Resource_need quantities. It has quantity space {Zero, Low, Medium, Plus}.

Prod_per_capita – This quantity is equal in purpose to the per capita birth rate of the single population. It represents the average birth or production rate per individual of the population. It has quantity space {Zero, Plus}.

Mort_per_capita – This quantity is equal in purpose to the per capita death rate of the single population. It represents the average death or mortality rate per individual of the population. It has quantity space {Zero, Plus}.

Open population quantities

Immigration – Like explained in the previous chapter, immigration represents the inflow of individuals of the same species, but from other populations, into the simulated population. This rate adds to the biomass of the population like the production rate does. It has quantity space {Zero, Plus}

Environment quantities

Resource_inflow – This quantity represents the constant inflow of resources into the environment. It is a static quantity and will not change. Its quantity space is {Zero, Low, Medium, Plus}

Resource_consumption – The population uses an amount of the resources in the environment. This quantity represents the amount of resources that the population consumes. Its quantity space needs to be equal to the Biomass and the Resource_inflow quantity and is thus {Zero, Low, Medium, Plus}.

Build_up_rate – This quantity is introduced to keep track of the result of the Resource_consumption subtracted from the Resource_inflow. It represents if the amount of resources available in the population will increase, stay the same or decrease. It has quantity space {Min, Zero, Plus}.

Resource_available – In the R-star model the population uses resources directly from what resources enter the environment. The Build_up_rate then determines whether some of the already available resources are needed or there will be some left to add to this stack. Dependent on whether this quantity increases or decreases, the production rate of the population will change in the same way. Its quantity space is {Zero, Low, Medium, Plus}.

Table 5.1 Quantities and quantity spaces as implemented in R-star model.

Quantity	Quantity space
Biomass	{Zero, Low, Medium, High}
Prod_per_capita	{Zero, Low, Medium, High}
Mort_per_capita	{Zero, Low, Medium, High}
Immigration	{Zero, Plus}
Resource_inflow	{Zero, Low, Medium, High}
Resource_consumption	{Zero, Low, Medium, High}
Build_up_rate	{Min, Zero, Plus}
Resources available	{Zero, Low, Medium, High}

5.1.3 Modelling assumptions

- **Assume full correspondence Available resources and prod per capita** – This assumption specifies that Resources_available and Prod_per_capita behave the same. Magnitude changes in one of both quantities will affect the other quantity in the same way.

- **Assume inflow consumption equal med value** – This assumption specifies that Resource_inflow and Resource_consumption are of comparable value by placing an equality statement between the Medium value in the quantity spaces of both quantities.
- **Assume constant resource inflow** – The derivative of the Resource_inflow quantity is zero which means it cannot change and is thus constant.
- **Assume no immigration** – This sets the immigration quantity and its derivative to zero, assuring no immigration takes place. This is not implemented as an assumption model primitive and thus will always be active.
- **Limited resource build up** – This will cause the Resources_available never to exceed the Medium value of the quantity space.
- **Assume constant mort per capita** – This sets the derivative of Mort_per_capita to Zero, making it constant and unable to change.

5.1.4 Model fragments

The R-star model contains 22 model fragments. An overview of all these model fragments is given in Figure 5.2. To make the comparison between the R-star model and the single population clearer, the model fragments of the R-star model will be described in a way similar to how the model fragments of the single population were described in the previous chapter. First the environment and all the fragments and assumptions relates to it will be described. Then, the population dynamics and the regulatory processes will be described. Thirdly, the usage of resources by the population will be described and lastly the model fragments related to an open population will be described.

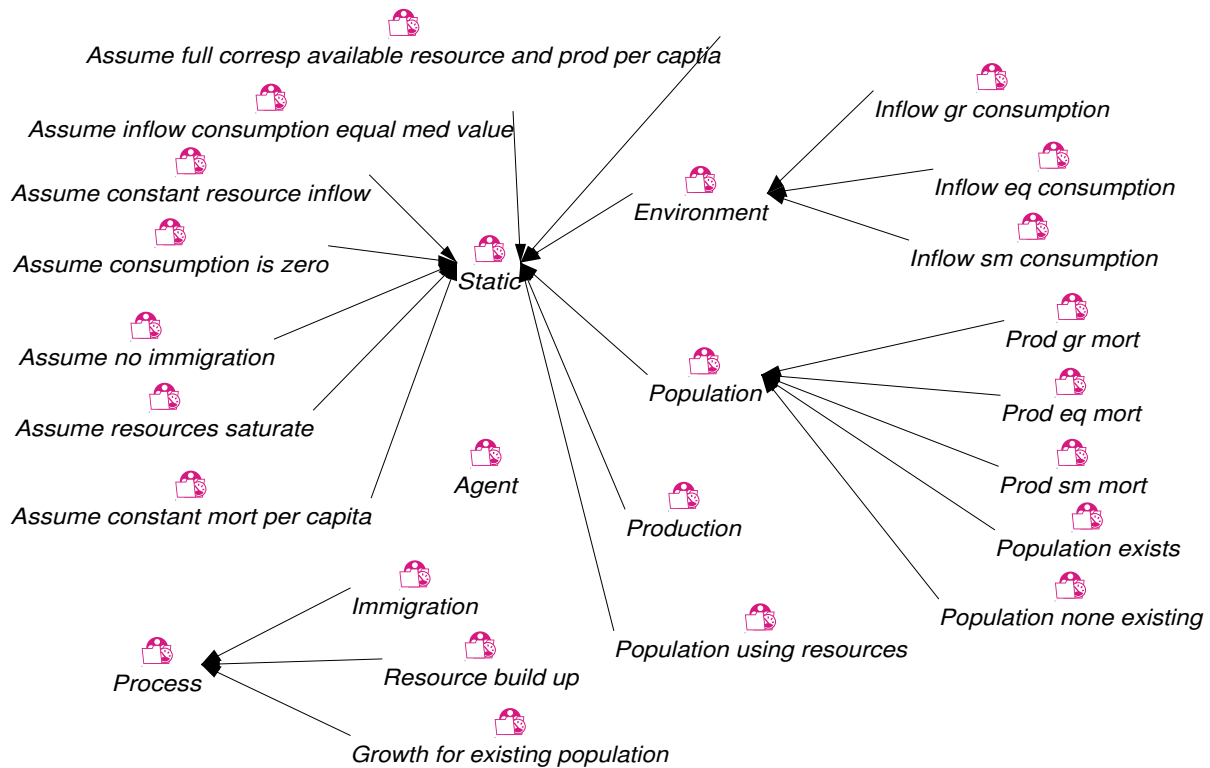


Figure 5.2: All model fragments in the R-star model.

Modelling the environment

The model fragments of the environment all begin with the static model fragment *Environment*. This fragment is shown in Figure 5.3. It includes an Environment entity as a condition and adds three quantities as consequences. These quantities are Resource_inflow, Resource_available and Resource_consumption. From this model fragment, three other static model fragments descend; *Inflow gr*

consumption, *Inflow eq consumption* and *Inflow sm consumption*, which all three include a different equality relation between *Resource_inflow* and *Resource_consumption*, equal to, greater than and smaller than (See Appendix D for a listing on these fragments).

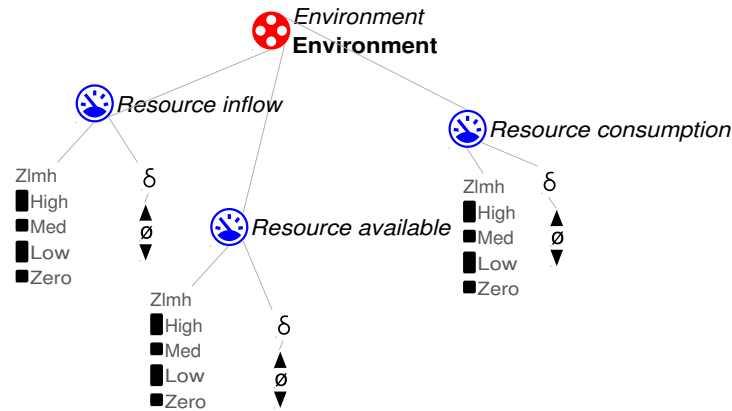


Figure 5.3: The *Environment* model fragment.

In the model fragment *Assume constant resource inflow*, the derivative of the quantity *Resource_inflow* is set to *Zero*, so it will remain constant. Although it is called an assumption, it does not implement an assumption which could be turned on and off by including it in a scenario (See Appendix D).

The *Resource build up* fragment, shown in Figure 5.4, is a process fragment and implements the dynamics of the environment according to the theory underlying the R-star model. In this fragment a new quantity, *Build_up_rate* is added as a consequence. The *Resource_consumption* quantity represents the amount of resources that is needed and used by the population. In a flow structure as used in the u-tube model and also in the Single population, the *Resource_consumption* is subtracted from the *Resource_inflow*. The result of this calculation is stored in the *Build_up_rate*, which can be *Min*, when the *Resource_consumption* is greater than the *Resource_inflow*, *Zero*, when both quantities are equal and *Plus*, when the *Resource_consumption* is smaller than the *Resource_inflow*. The *Build_up_rate* influences *Resource_available* positively, making it increase when *Build_up_rate* is positive and making it decrease when *Build_up_rate* is negative. *Resource_available* acts as a stack of resources from which sometimes resources are taken when the need exceeds the inflow and sometimes resources are added when the need is smaller than the inflow.

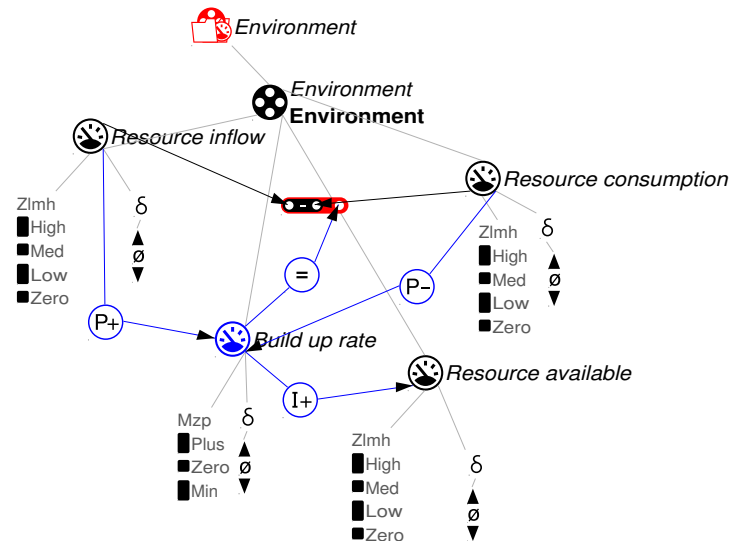


Figure 5.4: The *Resource build up* model fragment.

To reduce the ambiguity in calculating the difference between *Resource_inflow* and *Resource_consumption* the model fragment *Assume inflow consumption equal med value* defines an equality between the Med value in the quantity spaces of these quantities (see Appendix D). This knowledge can be activated using an assumption label ‘Med equality for inflow and consumption’ in the scenario.

The *Assume consumption is zero* and *Assume resources saturate* are not used in the scenarios, and their description will therefore be left out of this report.

When comparing the way the environment is modelled in the R-star model to the environment modelled in the Single population model, the first thing to be noticed is that the environment of the R-star model uses three more quantities, when including the *Build_up_rate*. The structure of the R-star environment includes a quantity which represents the need of the population. In the Single population model this quantity and the Min relation between what the population needs and the environment offers is created in a model fragment which includes both the environment and the population. In the R-star model, whether there are enough or insufficient resources, is calculated in the environment itself. Then the result of the equation is stored in the *Build_up_rate*, while in the Single population, the result is stored in the *Fulfilment_rate* of the population, because it sees the need and the fulfilment of that need as an aspect of the population. The R-star approach sees the result of the equation as an indication about how much resources are left in the environment. The *Resources_available* quantity represents this stack of resources.

Modelling the population dynamics and regulatory processes

The general population structure is modelled in the model fragment *Population*, shown in Figure 5.5, and this model fragment is also the parent for five other fragments. The *Population* fragment consists of the *Population* entity, added as a condition, with four associated quantities, added as consequences. These quantities are *Biomass*, *Prod_per_capita*, *Mort_per_capita* and *Immigration*. To make calculations about the differences between *Prod_per_capita* and *Mort_per_capita* less ambiguous, an equality relation is added between the Med values of both quantity spaces. It is conceptually clear that production and mortality rate are comparable quantities, so this ordinal relation does not need to be implemented as an assumption.

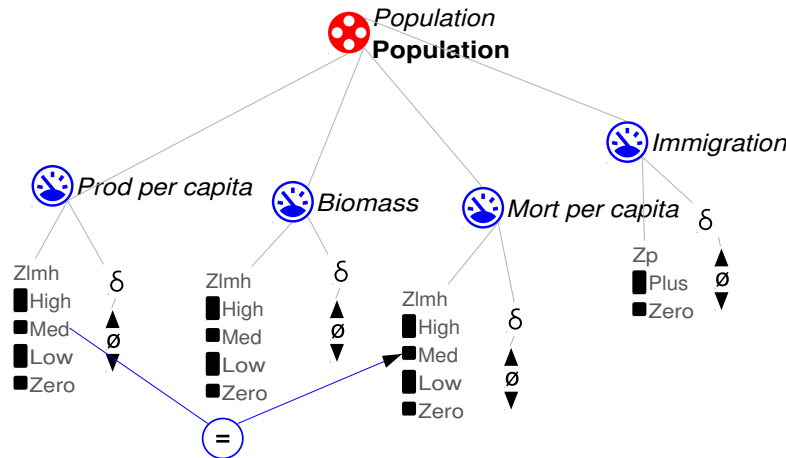


Figure 5.5: The *Population* model fragment

Similar to the single population model, the difference between an existing and a non-existing population need to be modelled. The model fragments that implement this difference are shown in Figure 5.6. The *Population exists* fragment implements a conditional inequality that is only true when *Biomass* has a magnitude higher than zero. The *Population none existing* model fragment implements the same kind of inequality, but instead sets the condition to be equal to zero so this model fragment will only be included by the reasoning engine when *Biomass* equals Zero.

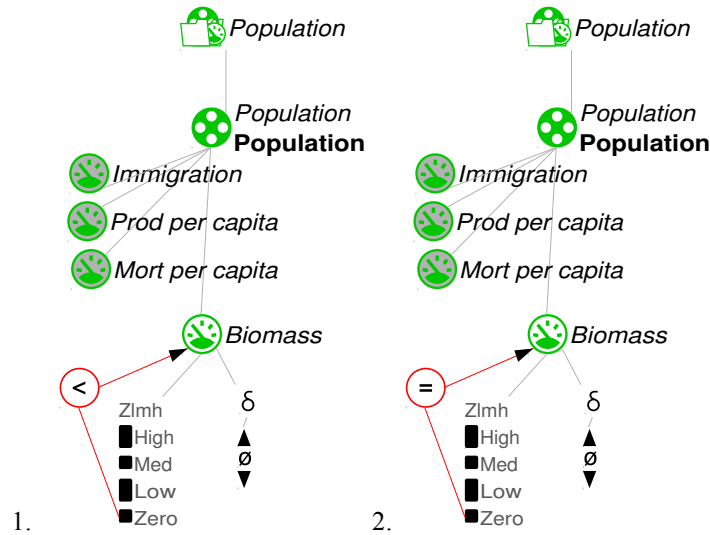


Figure 5.6: 1. The *Population exists* model fragment.
2. The *Population none existing* model fragment.

For the population dynamics to work, input is needed from the environment. With the configuration *Lives in*, it is structurally defined that the population lives in the environment. This is a condition for the *Production* model fragment, shown in Figure 5.7, to be added by the reasoning engine when running a simulation. The population is defined to be a plant species, which means that the Production model fragment only becomes active when the population lives in the environment and the Population entity is a plant species.

Prod_per_capita will change under influence of the positive proportionality from Resource_available. When Resource_available changes, Prod_per_capita will change in the same direction. The correspondence between the Zero magnitudes of both quantities will cause both quantities to become Zero when either one of them reaches Zero.

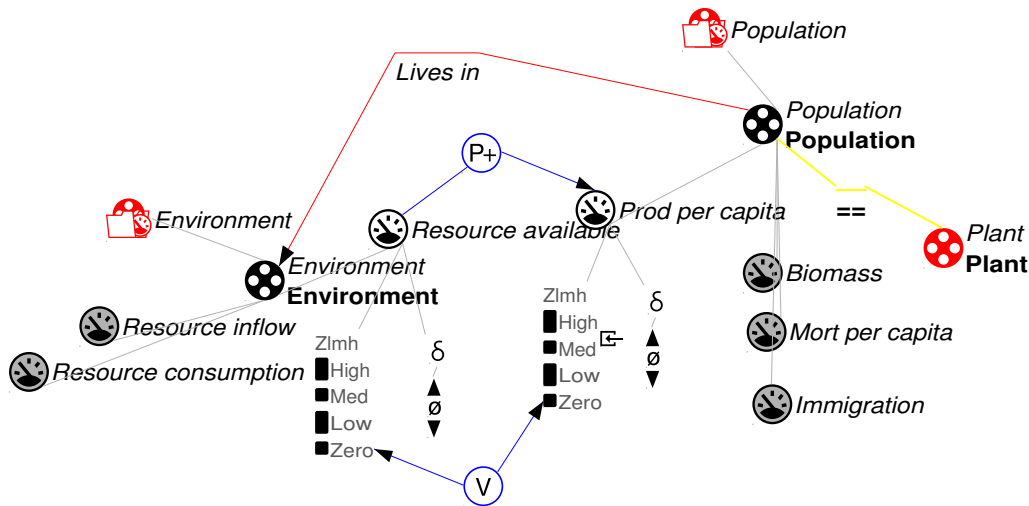


Figure 5.7: The *Production* model fragment.

When it is assumed that the production depends fully on the changes in the stack of food, a full correspondence can be added between Resource_available and Prod_per_capita. This causes both quantities to get the same values, when one of them changes without delays between states in the state-graph. This is modelled in the *Full correspondence available resources and production per capita* fragment (see Appendix D).

Mort_per_capita gets a constant value in the *Assume constant mort per capita* model fragment (see Appendix D). Its derivative is set to Zero as a consequence.

Biomass gets its value from a positive influence from Prod_per_capita and a negative influence from Mort_per_capita. Both influences are added as consequences in the model fragment *Growth for existing population*. This model fragment is shown in Figure 5.8 and will be included by the reasoning engine only when Biomass exceeds Zero, because a population can only grow when there are individuals that can reproduce.

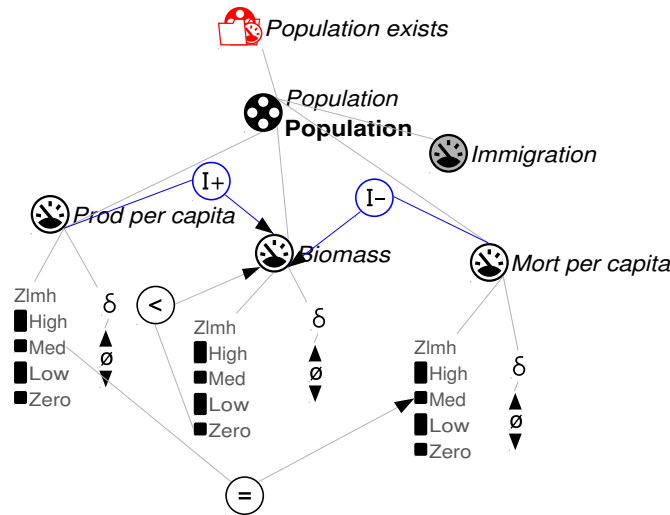


Figure 5.8: The *Growth for existing population* model fragment.

Comparing the way the population is modelled in the R-star model to the way used in the Single population, one of the things that is different is the manner in which the quantities are added to the population. In the R-star model all quantities are added in the first *Population* model fragment. In the Single population model, birth, death, immigration and emigration are added in their own model fragments instead of all at once. This is a difference in modelling practice and has no consequences for the dependencies that will eventually be included into the reasoning engine when running simulations.

Although the order in which the quantities are added to the population model fragments differs in the R-star model, the way to distinguish an existing population from a non-existing population is modelled in the same way, with equalities added as conditions.

The R-star model uses only two quantities to express a magnitude value of the population, the Biomass and the Resource_consumption, which is added to the environment. The Single population model uses Size, which expresses the number of individuals, and Biomass, which expresses the mass of the population in weight, and Resource_need, which expresses the energy need of the population. But the way these quantities gain their values is the same for the R-star population as for the Single population.

Modelling usage of resources by the population

The resource usage of the population is modelled by making the Resource_consumption quantity in the environment equal to the Biomass of the population. This is done in the same way as described in chapter 2, by adding a positive proportionality, an equality and a full correspondence between Biomass and Resource_consumption. The *Population using resources* model fragment is shown in Figure 5.9. As explained in the part of modelling the environment, the amount of resources the population needs are subtracted from the amount of resources that flows into the environment, in the model fragments that together make up the environment.

This is similar to the method used in the Single population model, which uses Resource_need that is kept equal to Biomass and Size, to indicate the amount of resources the population needs.

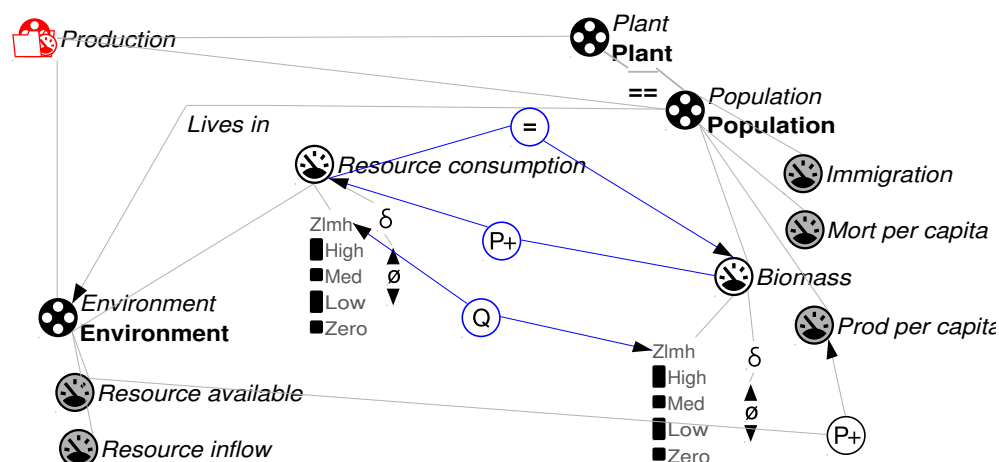


Figure 5.9: The *Population using resources* model fragment.

Modelling the open population

In the R-star model, the notion of an open population is modelled by using only Immigration. Immigration itself is modelled by a positive influence from Immigration, which was already added in the *Population* model fragment, to Biomass, as shown in Figure 5.10. The scenarios that will be shown in the next section, do not implement the immigration process, because the *Assume no immigration* model fragment sets Immigration and its derivative to Zero.

In the Single population model, the open population can be turned on and off in the scenarios by including or excluding the assumption *Assume open population*. The way Immigration influences the Biomass of the population is modelled in a similar way, although, unlike the R-star model, the Single population model also includes Emigration which exerts a negative influence on Biomass and Size.

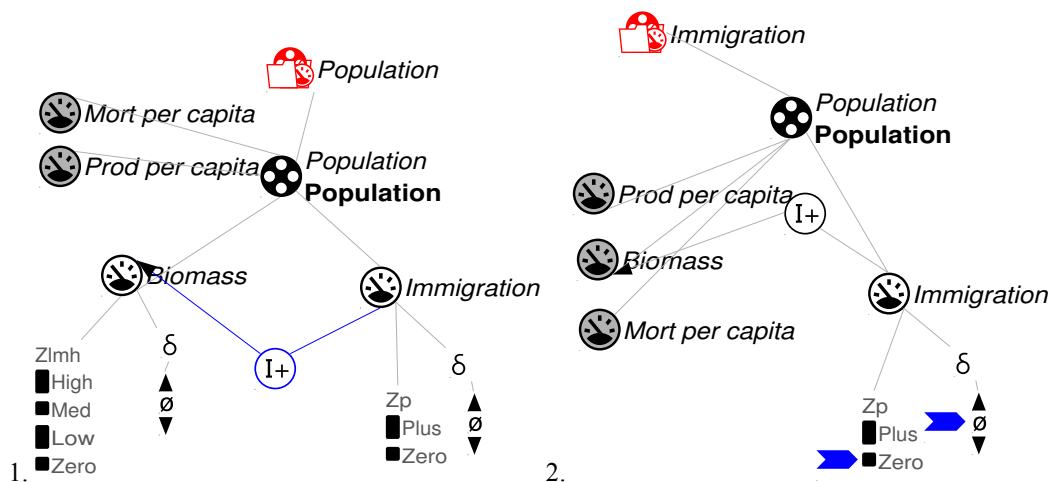


Figure 5.10: 1. The *Immigration* model fragment.
2. The *Assume no immigration* model fragment

5.2 Simulation of the R-star model

The R-star model includes five different scenarios. For the comparison of the single population and the R-star model two of these scenarios are selected. Similar to the single population, the results of the simulations ran on these scenarios will be analysed and evaluated.

5.2.1 Scenario 1: Population living in the environment

Scenario 1 of the R-star model is similar to scenario 2 of the single population and is shown in Figure 5.11. The population Biomass is given an initial Medium value and the Mort_per_capita which is constant, is set to Medium. It includes the assumption 'Full correspondence available resource and production per capita' which causes Prod_per_capita to react in the same way as Resource_available.

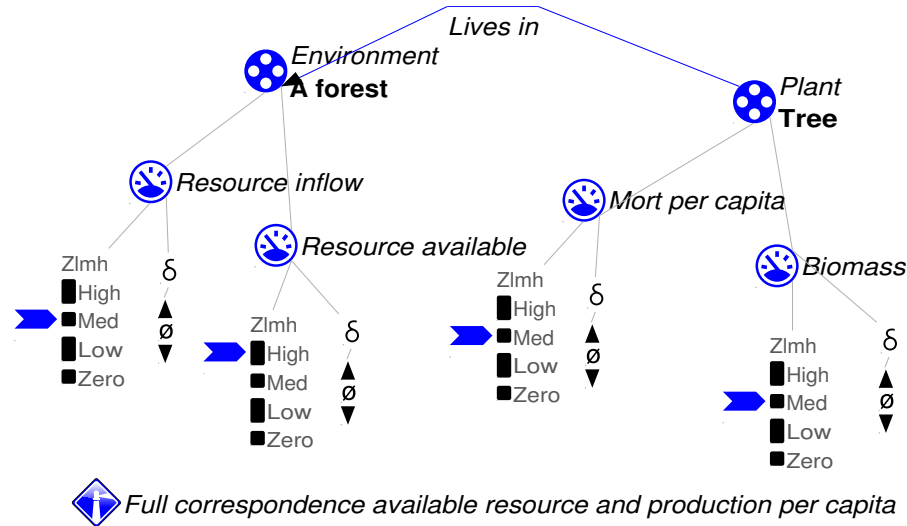


Figure 5.11: Scenario 1 of the R-star model.

Initial states

When simulating, the reasoning engine generates three initial states, as shown in Figure 5.12. In all states it can be inferred that Prod_per_capita, which is High just as Resource_available, is higher than Mort_per_capita. However, there is uncertainty about the equality relation between Resource_inflow and Resource_consumption. All possible equalities between Resource_inflow and Resource_consumption are tried and show as an initial state.

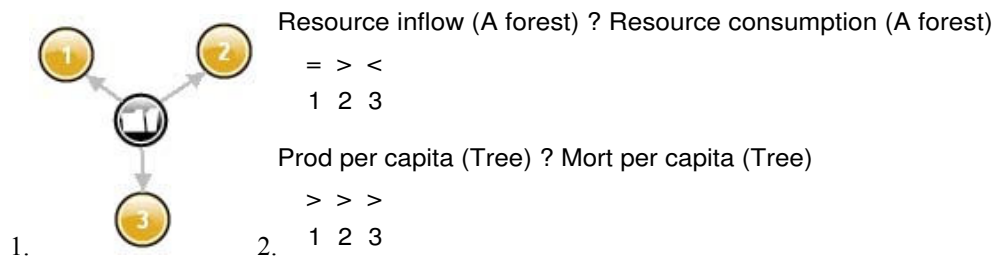


Figure 5.12: 1. The initial states of Scenario 1 of the R-star model.

2. The equation history of the initial states.

Because the outcome of the Min relation between Resource_inflow and Resource_consumption depends on the equality relation between those quantities, the quantity has a different Magnitude for all initial states, as shown in Figure 5.13. Because Prod_per_capita is higher than Mort_per_capita, Biomass is increasing in all initial states.

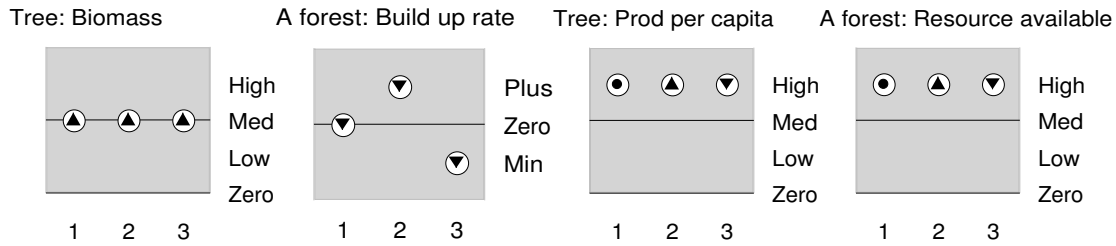


Figure 5.13: 1. The value histories for the initial states.

Behavioural paths

Figure 5.14 shows the complete state-graph for Scenario 1 of the R-star model. Similar to the *Population living in simple environment* scenario of the single population, the state-graph shows several interlinked cycles which can be followed as behavioural paths.

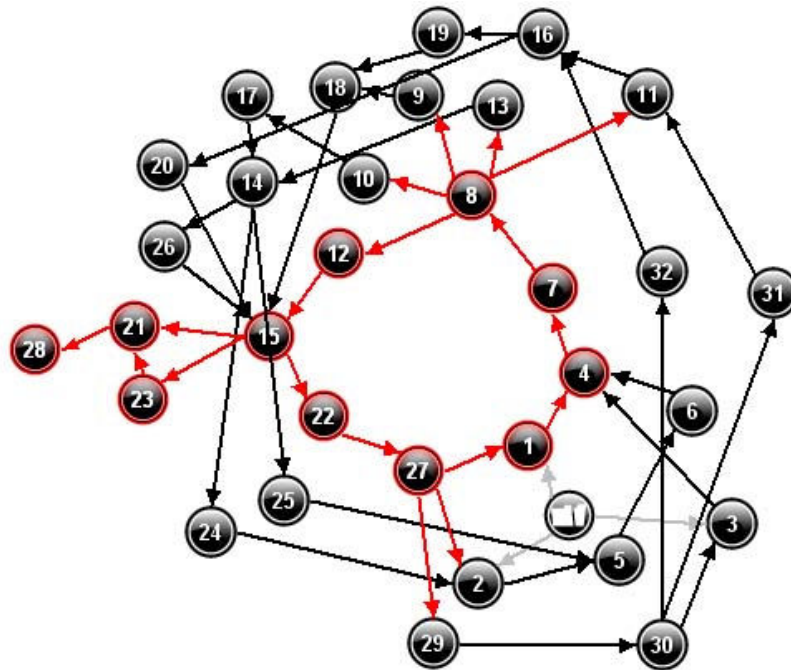


Figure 5.14: The complete state-graph of Scenario 1 of the R-star model with selected cyclic path {22,27,1,4,7,8,12,15,22} and ending path {22,27,1,4,7,8,12,15,22,23,21,28}.

There is also one ending path which can be reached via several possible cycles. The paths {22,27,1,4,7,8,12,15,22} and {22,27,1,4,7,8,12,15,22,23,21,28} are selected and can be investigated simultaneously because of their cyclic nature.

The value history is shown in Figure 5.15. At first, the Biomass is stable and Low in state 22. Because there are enough resources, as shown in Build_up_rate, the Prod_per_capita quantity increases which makes the Biomass increase also. At state 7, the Resource_available quantity reaches a magnitude where Prod_per_capita becomes equal to Mort_per_capita, which is stable and Medium. Biomass begins to decline from that point onward, until state 15, where the same mechanism again becomes active. There are enough resources, because the population has declined, and the Prod_per_capita quantity increases again, taking the behavioural path back to state 22.

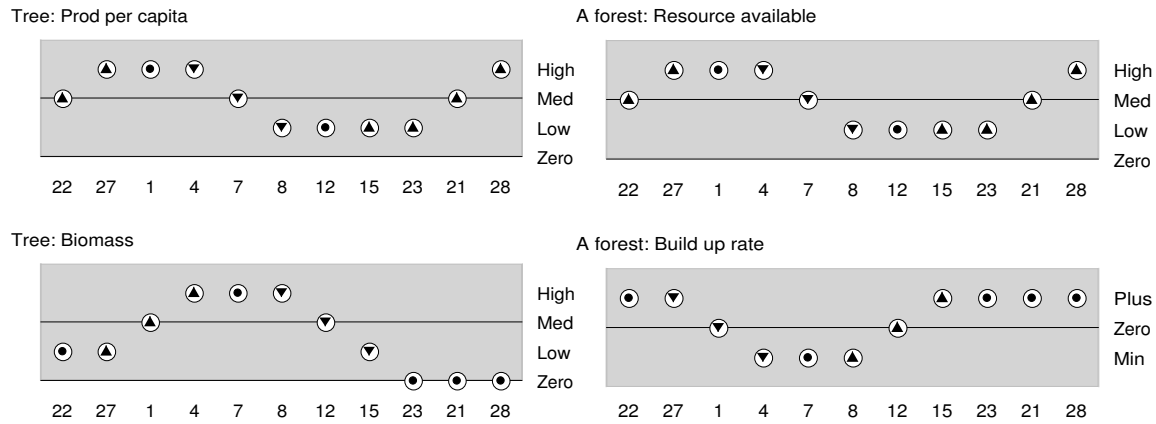


Figure 5.15: The value histories of the selected paths.

But, it can also happen that the population does not recover quickly enough from the setback of starvation. It then becomes extinct and Biomass reaches Zero. While the population Biomass is Zero, nothing reduces the amount of resources available and thus Resource_available reaches its maximum. Notice that it is conceptually incorrect that Prod_per_capita still increases after the population Biomass is set to Zero, for a population without individuals cannot reproduce. But this is a direct consequence of the assumption 'Full correspondence available resource and production per capita' which causes Prod_per_capita to react in the same way as Resource_available.

Figure 5.16 shows the equation history for the selected paths. It is correct that 22 and 7 are the states in which Prod_per_capita and Mort_per_capita become equal to each other and the equality relations shift, causing stabilization of the Biomass. Also, states 1 and 12 are states at which Resource_inflow becomes equal to Resource_consumption, and which cause stabilization of the Resource_available quantity¹.

Resource inflow (A forest) ? Resource consumption (A forest)

> > = < < < = > > > >
22 27 1 4 7 8 12 15 23 21 28

Prod per capita (Tree) ? Mort per capita (Tree)

= > > > = < < < < = >
22 27 1 4 7 8 12 15 23 21 28

Mort per capita (Tree) ? Prod per capita (Tree)

= < = > > > > = <
22 27 7 8 12 15 23 21 28

Biomass (Tree) ? Zero

> > > > > > > = = =
22 27 1 4 7 8 12 15 23 21 28

Figure 5.16: The equation histories of both selected paths.

¹ A side note on the equation history is that there are two equality relations between Prod_per_capita and Mort_per_capita, as shown in the Figure. Only the equality relation from Mort_per_capita to Prod_per_capita becomes active after state 6, on state 7. However, it does not interfere with the correctness of the behaviour and is caused by the Garp3 software package.

End states

There is only one end state in the state-graph of this scenario, which is state 28. The population Biomass has gone to Zero in state 23, so the end state does not only describe that the population has gone extinct. In the end state the Resource_available quantity has reached its maximum value and thus the behavioural path has reached a point where no more changes can be derived from the model fragment library.

The causal model

From the model fragment library, two kinds of causal models are derived in the path {22,27,1,4,7,8,12,15,22,23,21,28}. In Figure 5.17, the first diagram describes the system structure when the Biomass is higher than Zero and the other diagram describes the system structure when the Biomass is equal to Zero.

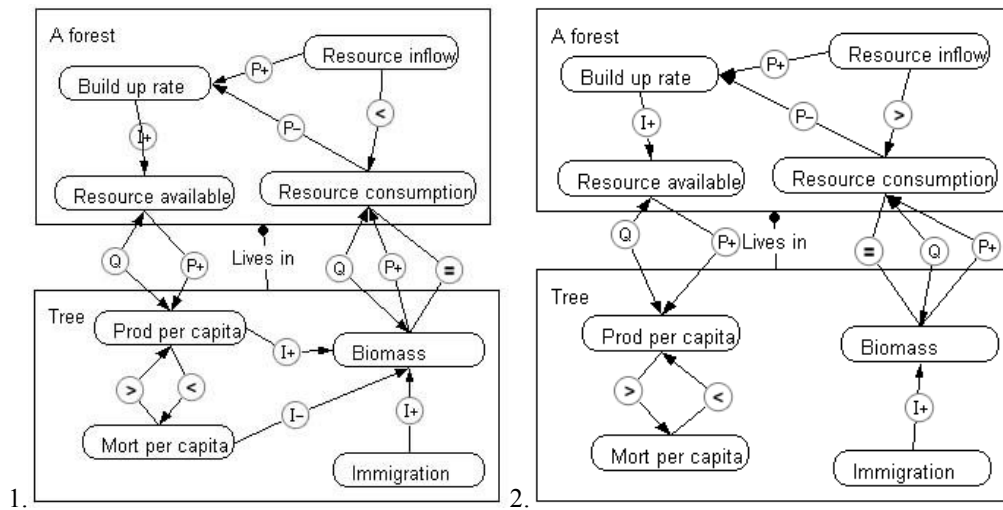


Figure 5.17: 1. Dependencies in state 8 of the state-graph of Scenario 1
2. Dependencies in state 28 of the state-graph of Scenario 1

The dependencies in the states 23, 21 and 28 have the format of the second diagram of Figure 5.17. In these states, Biomass is Zero which deletes the direct influences from Mort_per_capita and Prod_per_capita. The rest of the system structure is the same as when the Biomass is higher than Zero. For both Figure it seems that the system structure is derived correctly from the model fragments library.

5.2.2 Scenario 2: Population living in the environment with added equality

Scenario 2 is similar to Scenario 1 and is comparable to Scenario 3 of the single population, which is described in the previous chapter. As shown in Figure 5.18, an assumption 'Med equality for inflow and consumption' is added to the scenario, which reduces ambiguity in the simulation by making the quantity spaces of Resource_consumption and Resource_inflow comparable. The magnitude of Resource_inflow can be varied to create different initial conditions.

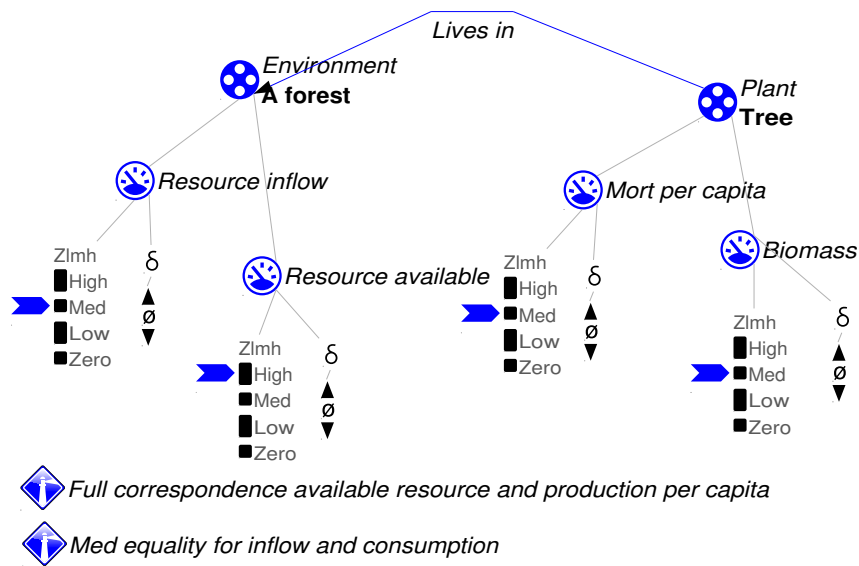


Figure 5.18: Scenario 2 of the R-star model

Initial states

The simulation starts with one initial state, as shown in Figure 5.19. This is the direct effect of the assumption added to the scenario, which reduces the possibilities from three initial states in scenario 1 to only one in this scenario. Now the reasoning engine can deduce directly that a Medium Resource_inflow and a Medium Biomass means that Resource_inflow and Resource_consumption are equal to each other, which means only one possible value for Build_up_rate instead of three in scenario 1.

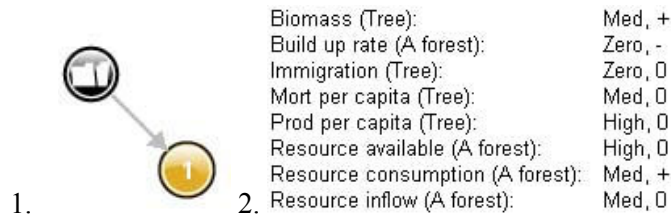


Figure 5.19: 1. The initial state of the simulation of scenario 2 of the R-star model.
2. The quantity values of the initial state of the R-star model.

Behavioural paths

Figure 5.20 shows the complete state-graph of scenario 2 of the R-star model. The state-graph of this scenario also shows similarities to the state-graph of scenario 5 of the single population model, which is comparable to this scenario. It shows two possible cycles, which are slightly different, and one possible ending path.

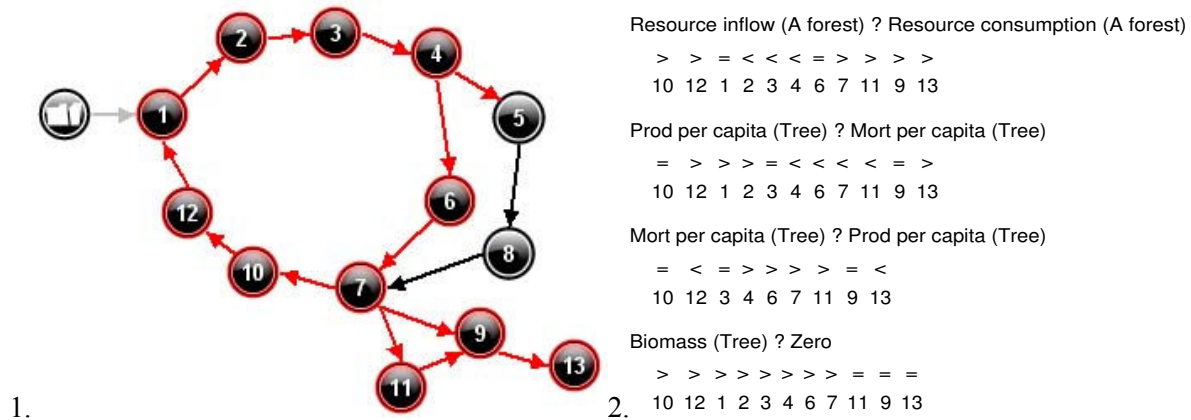


Figure 5.20: 1. The full state-graph of the simulation of scenario 2 of the R-star model with selected cyclic path {10,12,1,2,3,4,5,6,7,10} and ending path {10,12,1,2,3,4,6,7,11,9,13}.
2. The equation history of the selected paths.

Figure 5.20 also shows the equation history of the paths which are selected in the state-graph. Together with the value histories shown in Figure 5.21 its possible to see that the behaviour paths in the state-graph of scenario 2 are correct.

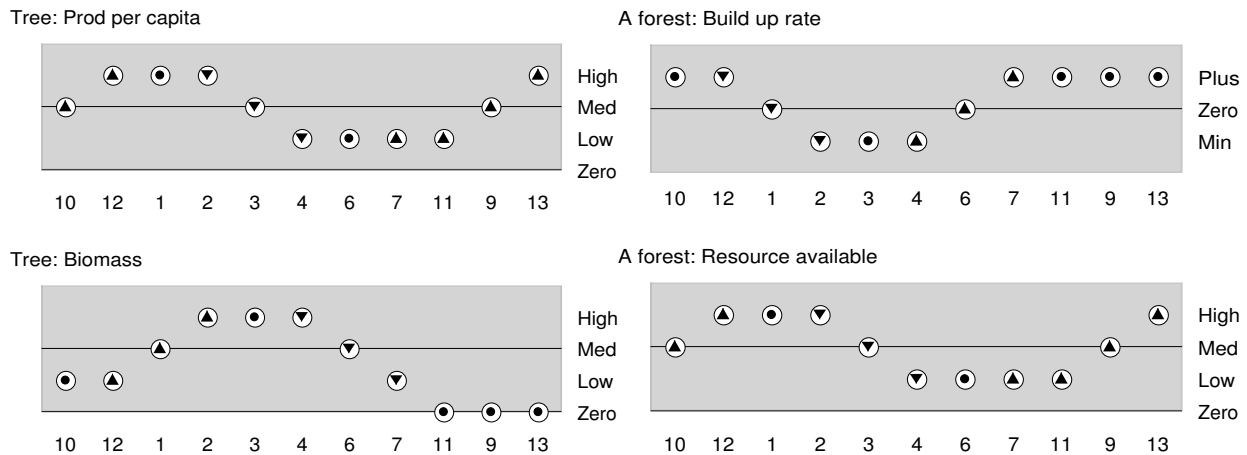


Figure 5.21: The value histories of the selected cyclic path {10,12,1,2,3,4,5,6,7,10} and ending path {10,12,1,2,3,4,6,7,11,9,13}.

As in scenario 1, Prod_per_capita first increases to a point, reached in state 1, where it cannot be supported by the environment anymore and starts to decrease. Then, when Mort_per_capita exceeds Prod_per_capita, which happens in state 3, the Biomass starts to decrease. With the decrease of Biomass, there comes a point where the environment can support the population again, and after state 6, the Prod_per_capita starts to increase again. From this point, Biomass is still decreasing because it may take a while before births exceed deaths again, two things can happen. The population may go extinct, and it can go back towards state 10 and start growing anew.

When it goes extinct, this happens in the same way as in scenario 1 of the R-star model. Resource_available will increase in three successive states and Biomass will remain Zero. This reflects the same conceptual flaw as in scenario 1, that Prod_per_capita increases with Resource_available when the Biomass has reached Zero.

End states

The end state of this scenario is state 13 and has the same qualities as the end state of scenario 1.

The causal model

The dependencies are also the same as in scenario 1, like shown in Figure 5.17.

5.3 Concluding remarks

The R-star model will not be evaluated on its strengths and weaknesses, but compared to the single population model which is constructed for this thesis. As was mentioned in section 5.2, there are several important differences between the R-star model and the Single population model presented in chapter 4.

5.3.1 Differences in assumptions

The R-star model assumes a constant death or mortality rate, which is not influenced by the varying amounts of available resources in the environment. Conceptually, the actual growth of a population is not only determined by the production rate, because mortality rate is also influenced by the resources in the environment. But, like argued in the Single population modelling choices, the most important influence on growth is the changing equality relation between production and mortality rates. When mortality is considered to be stable, the changing production rate will still cause this equality relation between production and mortality to change.

Furthermore the R-star model assumes that the production or birth rate of the population rises and falls with the available resources in the environment. This is a difference in approach between the R-star model and the Single population model. The production rate represents a potential for reproduction and this is influenced by whether the amount of resources in the environment can fulfil the needs of the population. This also explains the behaviour observed that the *Prod_per_capita* rate is allowed to grow with the *Resource_available* even after the population has gone extinct. The resources available in the environment mean that there is still potential for the population to reproduce, not the fact of the population exists or not.

5.3.2 Differences in modelling choices

The most important difference between the qualitative models is the way in which the environment is modelled. The R-star model models the environment according to the notion that within the environment there is a mechanism which indicates how much resources there are left. This amount is calculated and stacked in another quantity. From this stack, resources are used when the resource need of the population in the environment exceeds the inflow of resources in the environment. This stack represents the actual available resources and influences the changes in production directly.

An advantage of this approach is that multiple producer populations can live in the same environment, provided that their need of resources is combined in the resource need quantity of the environment. But both populations will then change and grow in the exact same way, if both their production rates change with the available resources in the environment.

Also, conceptually this approach could be a more accurate description of the real situation in the environment, instead of just assuming the resources in the environment to be constant. But it is not specified in the theory that a stack of resources is kept in the environment which determines the potential for reproduction or if the population keeps track of this potential in a fulfilment rate.

But if the population does not include an indication whether or not its resource need is fulfilled, it is more difficult to re-use the model when building models including multiple populations. *Build_up_rate* determines the regulatory process and initiates starvation, but has no place in the population. When an additional population would be added to the R-star model, where would the calculation take place that determines whether there is enough prey for the predator?

The difference in modelling practice can be explained by the difference in purpose for both models. The Single population is designed to be compact and reusable, whereas the R-star model aims at researching how systems which exhibit high degrees of uncertainty can be captured in a qualitative model.

5.3.3 Differences in implementation

Although the way the environment and the population are implemented in the R-star model does not look similar to the way the Single population is modelled, when looking closer, there are a lot of similarities. The Resources_available quantity represents a stack of resources, but its derivative will be equal to the magnitude of Build_up_rate, because of the direct influence between those two. In the Single population, Fulfilment_rate represents the same calculation result as shown in Build_up_rate and a direct influence is created from Fulfilment_rate to the per capita birth- and death rates. Since the Resource_available quantity is made to correspond with the Prod_per_capita quantity in the R-star model, the mechanisms used in both models are in fact the same, but represent different things. The final differences in simulation results between both models are a consequence of the other minor differences in implementation that were observed in this chapter.

5.3.4 Evaluation

When comparing the Single population model developed in this thesis to the R-star model, it can be observed that although there are several differences in approach and implementation, both models have a lot in common. Although the models have been developed independently from each other and for different purposes, the same theoretic principles are captured in both models and the behaviour shown in similar scenarios matches almost perfectly.

6. Modelling predation

6.1 Introduction

In this section, the single population model constructed in chapter 4 is used to construct a more extensive model which includes predation. Predation links together the populations that are part of a food chain, as described in chapter 3. A food chain consists of multiple species populations which all predate on the subsequent layer below them in the trophic structure. The presented model of predation includes two populations in one environment, whose internal dynamics are comparable, and in which one is the prey and the other is the predator.

The theory specifies that internal processes still operate within each population when it is involved in an interactive process with another population. Whether a population is a prey or a predator or both at the same time, its internal make-up is the same. Predator and prey populations have the same properties, but the sources they use for food and the effect they have on the environment are different.

In previous work, several qualitative models of two populations have been constructed already (Salles et al., 2003) (Nuttall et al., 2004), but none of these models implement the Single population dynamics as described in chapter 4.

6.1.1 Detailed description of the system

There are two populations living together in one environment. The prey population draws its resources directly from the environment, like the scenarios included in the single population model. The predator population depends on the prey populations for its resources, and gains its energy by consuming individuals of the prey population. It is common for prey populations to have a higher biomass than the predator population, but even so, the prey can be small or big compared to the predator population. This is because although a prey population may have a higher biomass, its biomass can still be insufficient for the predator population to sustain itself with. In the beginning of the scenario discussed here, the biomass of the prey population is big enough to sustain the predator population.

Predation causes more individuals of the prey population to die, increasing the death rate and decreasing the birth rate of the prey population. After some time deaths will exceed births and the prey population size will start to decline under influence of predation.

In the predator population the birth rate increases because it has access to enough resources to sustain and grow. This will cause births to exceed deaths and the population size to increase.

After some period of time the biomass of the prey population has declined to a level where it is not big enough to sustain the larger predator population anymore. The regulatory processes of the predator population will become active and individuals will begin to die because there is not enough prey to be found and only the fastest and strongest will have access to enough food. Eventually this increased death rate in the predator population causes deaths to exceed births, making the predator population decline in size.

This decline of the predator population means that the effects of predation on the prey population diminish. The death rate of the prey population declines and after some time births will again exceed deaths. This allows the prey population to grow again. The growth of the prey population and the decline of the predator population means that there will come a moment in time that the prey population has grown to a size which can support the smaller predator population again. This is a return to the initial state of the scenario.

The lag between predator and prey population in the propagation of the effects of resource shortage can be explained by the time it takes organisms of each population to reproduce.

6.1.2 Modelling goal

The goal of this modelling task is to construct a model of predation which is an extension of the single population model created in the chapter 4. This model of predation should be able to be reused when modelling the interactions between populations and eventually food chains and food webs.

6.2 Creating the causal model

6.2.1 Identifying the processes

The internal population processes are the same as those distinguished in chapter 4.

Interaction between species

Predation – The act of one population of species using another population of species as source of food by eating the prey in the process is called predation. Predation actually increases the death by predation factor of the prey population and thus increases the death rate. The other way around it influences the birth process of the predator population positively. Predation can only occur when there is a prey population with enough biomass to sustain the predator population with energy.

6.2.2 Modelling choices

Using the internal dynamics of the Single population model

When re-using the Single population model, the causal model of predation would logically look as shown in Figure 6.1. But although the Single population is a simple model and its simulation results, in the third scenario, are unambiguous, two inequalities changing constantly in more than one population, cause too much ambiguity in a simulation. To solve this, the equality relation between births and deaths is transformed into a growth rate. The growth rate will determine whether the population grows or declines in size in the adapted model.

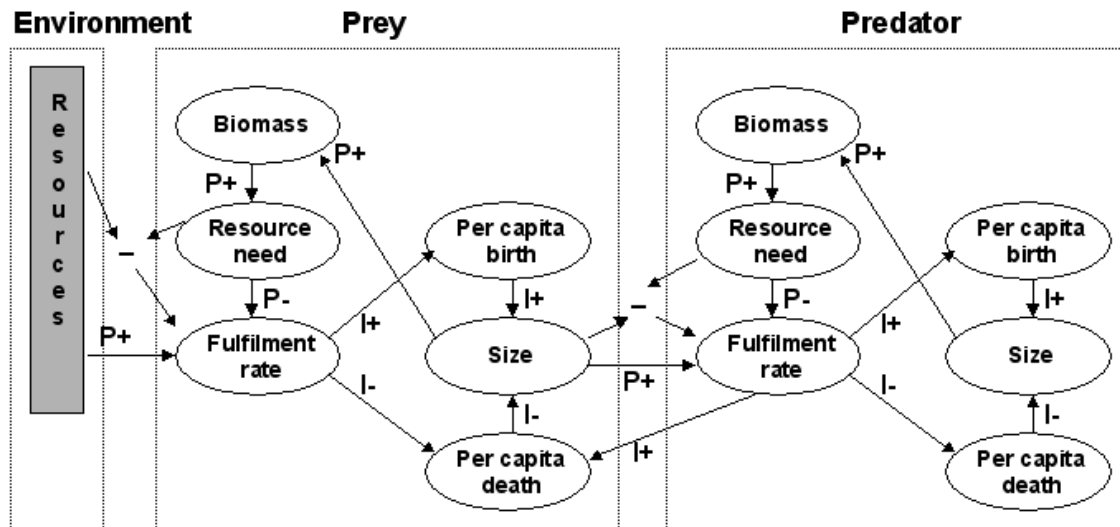


Figure 6.1: the Causal model of predation re-using the Single population.

In the previous chapter, it became clear that the R-star model and the Single population model have some similarities. In this light, the environment of the Predation model can be modelled as shown in the R-star model without truly changing the approach followed in the Single population model. The use of a stack of available resources will be useful to determine the value of the growth rate which can be calculated by determining whether the value of the available resources can supply the need of the population in the future. The resulting causal model is shown in Figure 6.2.

population to become extinct by heavy predation of the predator. This will eventually also result in the extinction of the predator population as it is dependent on the availability of prey for its survival.

6.3 Implementation

6.3.1 Structural details

Entities

The predation model needs three entities:

Population/Prey/Producer: A producer population is capable of reproducing, growing and producing oxygen by using nutrients from the soil and sunlight. Most of these species are plants. They provide most of the energy for the successive layers of species of a food chain by being preyed upon by herbivores.

Population/Predator/Consumer: A predator feeds on individuals of another population to gain energy through nutrition. Herbivores are also considered to be predators.

Environment: An environment is the situation in which communities and thus populations of species live. Environments can be further divided into habitats, pieces of environments that meet the specific needs of a population.

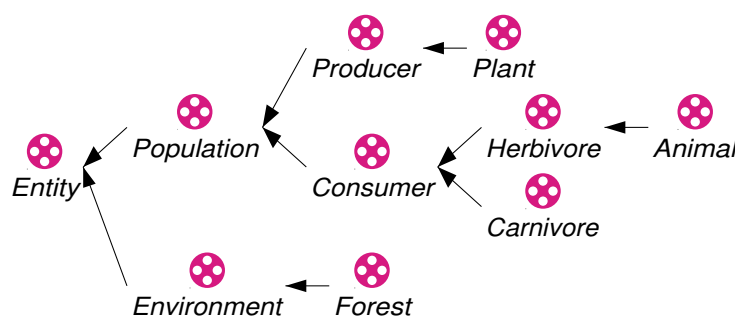
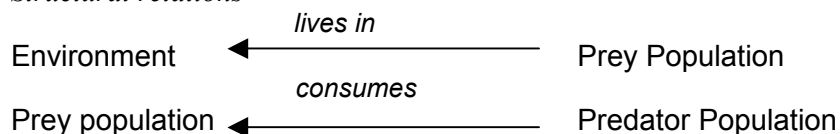


Figure 6.3: Entity relationship diagram of the Predation model.

Structural relations



The Predation model adds one structural relation to the Single population model: the *consumes* configuration. This describes that the source population uses the target population as its source of food.

6.3.2 Quantities and quantity spaces

Predator and Prey Population

Size – Like in the Single population, Size represents the number of individuals in the population.

Biomass – Also, like in the Single population, Biomass represents the total mass of all the individuals in the population.

Resource_need – Resource_need represents the energy and nutrient need of the population.

Growth – Instead of using birth- and death rates, Growth is introduced. This quantity indicates whether the population is increasing, decreasing or stable.

Environment

Resource_available – As in the R-star model, this quantity describes a stack with an amount of resources that is left in the environment.

Resource_inflow – Also, as in the R-star model, this quantity describes the inflow of resources into the environment.

Build_up_rate – The Build_up_rate is the equivalent of the Fulfilment_rate used in the Single population model and it describes whether the need of the population could be fulfilled or not. In this model and the R-star model it also describes whether the amount of resources that is available in the environment increases or decreases.

Resource_consumption – This quantity is equal to the Resource_need quantity of the population and describes how much of the resources are consumed by the population.

Table 6.1: the quantities and their quantity spaces in the predation model.

Quantity	Quantity space
Size _{prey} , Size _{predator}	{Zero, Low, Medium, Plus}
Biomass _{prey} , Biomass _{predator}	{Zero, Low, Medium, Plus}
Resource_need _{prey} , Resource_need _{predator}	{Zero, Low, Medium, Plus}
Growth _{prey} , Growth _{predator}	{Min, Zero, Plus}
Resource_available	{Zero, Low, Medium, Plus}
Resource_inflow	{Zero, Low, Medium, Plus}
Resource_consumption	{Zero, Low, Medium, Plus}
Build_up_rate	{Min, Zero, Plus}

6.3.3 Assumptions

Theoretical assumptions

- The environment is closed.
- All populations are closed.
- There is a constant amount of available resources.
- Only predation and the internal regulatory processes cause the birth- and death rates to change.

Modelling assumptions

- **Assume biomass and resource need correspondence** – This assumption describes that there is a full correspondence between the Biomass and Resource_need quantities. In the Single population model it was also assumed that these quantities behaved in the same way.
- **Assume size and biomass correspondence** – This assumption describes that there is a full correspondence between the Size and Biomass quantities. In the Single population model it was also assumed that these quantities behaved in the same way.
- **Assume constant resource inflow** – As in the Single population and the R-star model, the inflow of resources in the environment is considered to be constant.
- **Assume med equality between available and need** – The medium equality between Resource_available and Resource_need makes the result of the subtraction between those quantities more decidable and thus reduces ambiguity.

6.3.4 Model fragments

In theory it should be possible to completely re-use the model of the single population described in the previous section, but when adding only one model fragment which describes two populations predating on each other, the ambiguity becomes too large, preventing easy insight in the behaviour that results from the simulation. That is why in the modelling choices several refinements on the original concept of the single population have been made. A complete overview of the model fragments in the Predation model is given in Figure 6.4

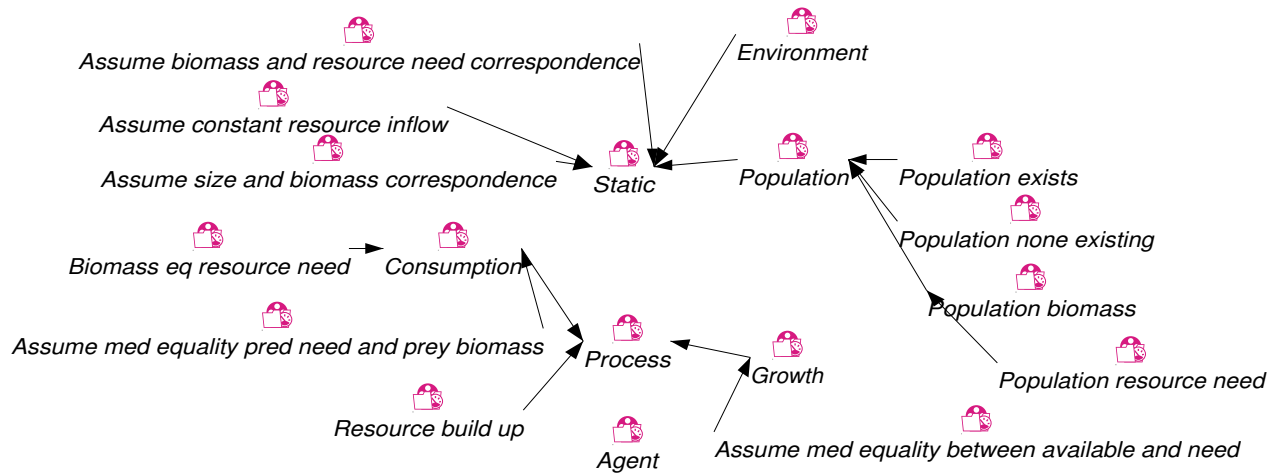


Figure 6.4: The model fragment overview of the Predation model.

Modelling the environment

The environment in the predation model is modelled as in the R-star model. The *Resource build up* fragment is similar to the fragment with the same name from the R-star model and shown in Figure 6.5.

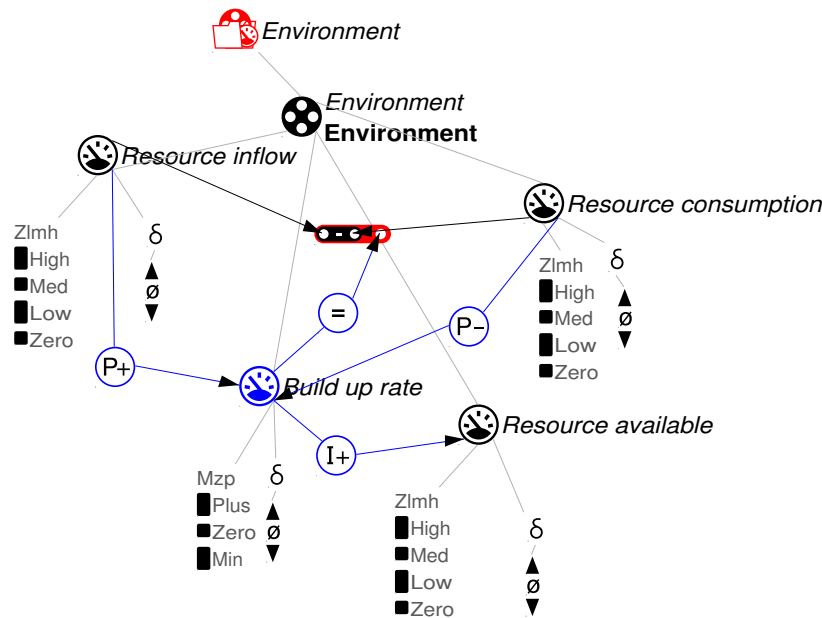


Figure 6.5: The *Resource build up* fragment.

Also important for the environment is the assumption that the *Resource_inflow* quantity is constant. This assumption is implemented by setting the derivative of *Resource_inflow* to Zero as a consequence of implementing the assumption in the reasoning engine.

Modelling the notion of population growth

When looking at the way the population is modelled in the Predation model, it is equal to the way the population is modelled in the Single population model, except for *Fulfilment_rate*, which is now represented as *Build_up_rate* in the environment, and birth and death rates, which are replaced by growth. There are full correspondences assumed between *Size*, *Biomass* and *Resource_need* to create decidable results when doing calculations. The model fragment *Growth* is shown in Figure 6.6.

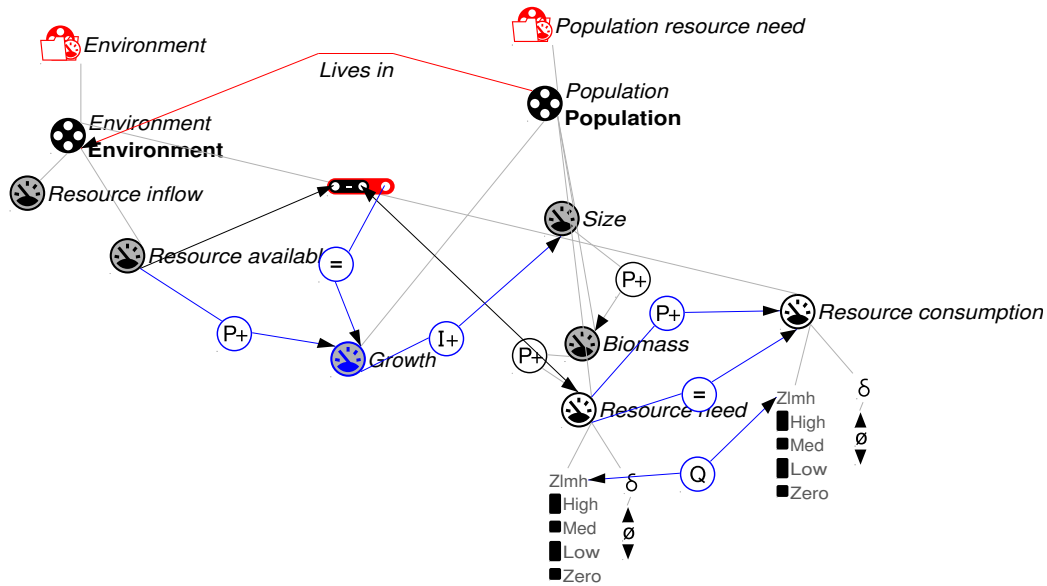


Figure 6.6: The *Growth* model fragment.

Because the environment is modelled in a similar way to the R-star model, the *Resource_consumption* quantity of the environment needs to get its value from a full correspondence, a proportionality and an equality relation with the *Resource_need* quantity of the population.

Resource_available represents the amount of resources that are left in the environment when the population has taken what it needs. To give the *Growth* its value, it must be known if the population can grow or if there are not enough resources left. This value is calculated by a min relation between the *Resource_available* and *Resource_need* quantities. *Growth* then gets the value of its derivative from *Resource_available* and will change in the same direction because of a positive proportionality. From *Growth* there is a direct positive influence on *Size* of the population. An equality is assumed between the Medium values of *Resource_available* and *Resource_need* in the model fragment ‘Assume med equality between available and need’. As in the Single population and the R-star model this serves to reduce ambiguity.

Modelling predation

To model predation, the *Consumption* model fragment, shown in Figure 6.7 is introduced.

correspondence', 'Assume full biomass and resource_need correspondence' and 'Assume med equality between available and need'.

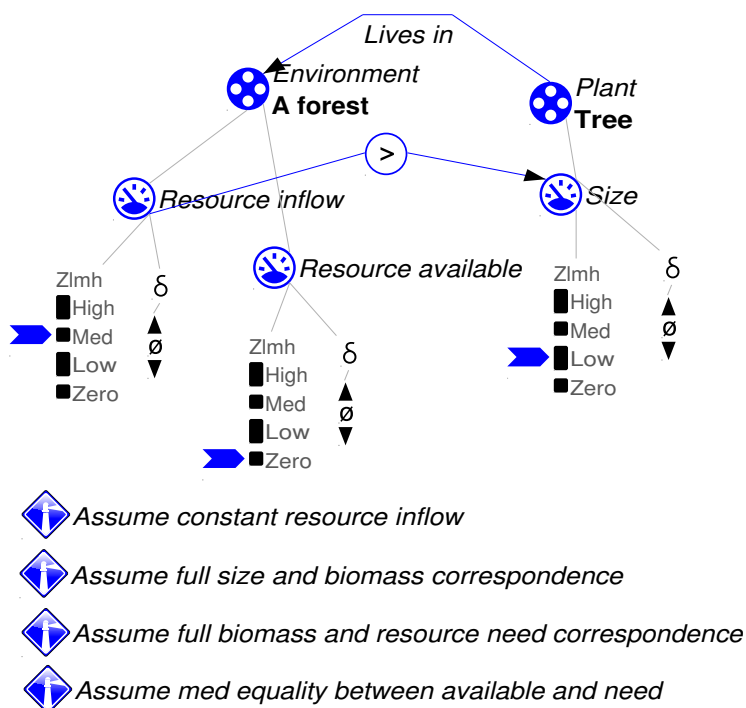


Figure 6.8: Scenario 1: The single population with adaptations.

Initial states

Simulation of the first scenario of the predation model results in only one initial state. Figure 6.9 shows that there are enough resources for the population in this state, because the Build_up_rate is Plus and increasing. The Growth starts at Min, because the Resource_available quantity is Zero and the Resource_need is equal to Size and thus Low.

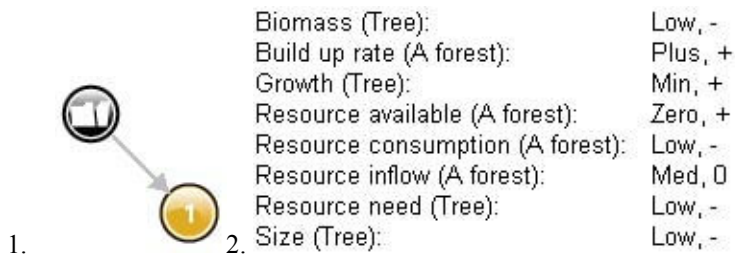


Figure 6.9: 1. The initial state of Scenario 1 and
The quantity values of the quantities in the initial state of Scenario 1.

Behavioural paths

Figure 6.10 shows the complete state-graph of this scenario. It shows a circular behavioural path, which suggests cycling behaviour as in the Single population model. The equation history for the equality relation between Resource_inflow and Size is also shown in Figure 6.10. This equality relation is the most important for it determines the magnitude of Build_up_rate.

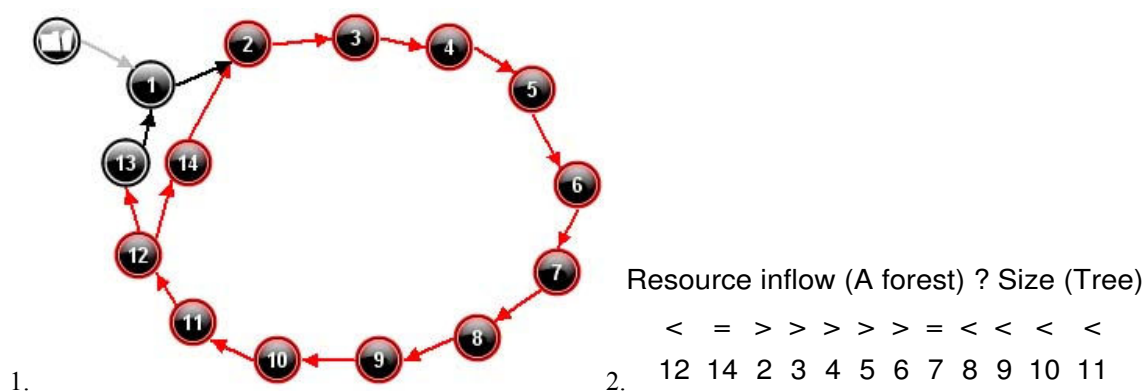


Figure 6.10: 1. The complete state-graph of Scenario 1 with selected cyclic path {12, 14, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11}.
2. The equation history for the selected path

The equation history confirms that the state-graph exhibits cycling behaviour. By investigating the value history, as shown in Figure 6.11, the cycling behaviour can be observed. The Size of the population decreases because there are not enough available resources. In state 2 through 6, the Build_up_rate is Plus, meaning there are enough resources. This is when the population Growth increases to Plus. It takes a while before the Size responds to the Growth rate and Size increases to High. When Size is increasing in state 7, the amount of available resources is not sufficient anymore and begins to decrease. This is also reflected in the Growth rate which causes Size to stabilize in state 9 and to decrease in state 10. Then Size decreases in state 9 through 2, in which the resources are replenished in Build_up_rate. This results in stabilization of Size in state 3, and the growth of the population to start over.

Similar to the Single population model, the behaviour shown in this adapted version also reflects the observations in ecology theory.



Figure 6.11: The value history of the selected path.

The causal model

Because of the adaptations made to the Single population causal model, the dependencies of the predation model, as shown in Figure 6.12, partially differ from those observed when simulating the Single population model. But the dependencies shown in the Figure match the system structure implemented in the model fragment library.

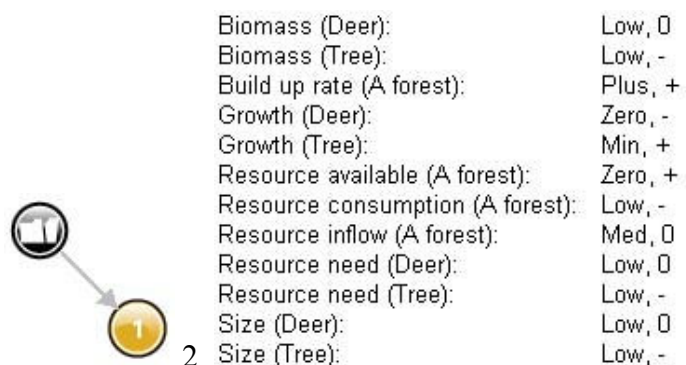


Figure 6.14: 1. The initial state of Scenario 2.
2. The quantity values of the quantities in the initial state of Scenario 2.

Behavioural paths

When fully simulating the scenario, the resulting state-graph is large. This means many possible behavioural paths and some ambiguity. Still, this is an insightful result. As shown in Figure 6.15, there are many possible behavioural paths that can be investigated. Consider for instance the one at the centre of the graph. The path {6, 10, 14, 19, 21, 24, 28, 38, 40, 57, 59, 4} is a cycle and when the state-graph is inspected more closely, many paths can be found that lead to and from this cycle, most of which form longer cycles themselves.

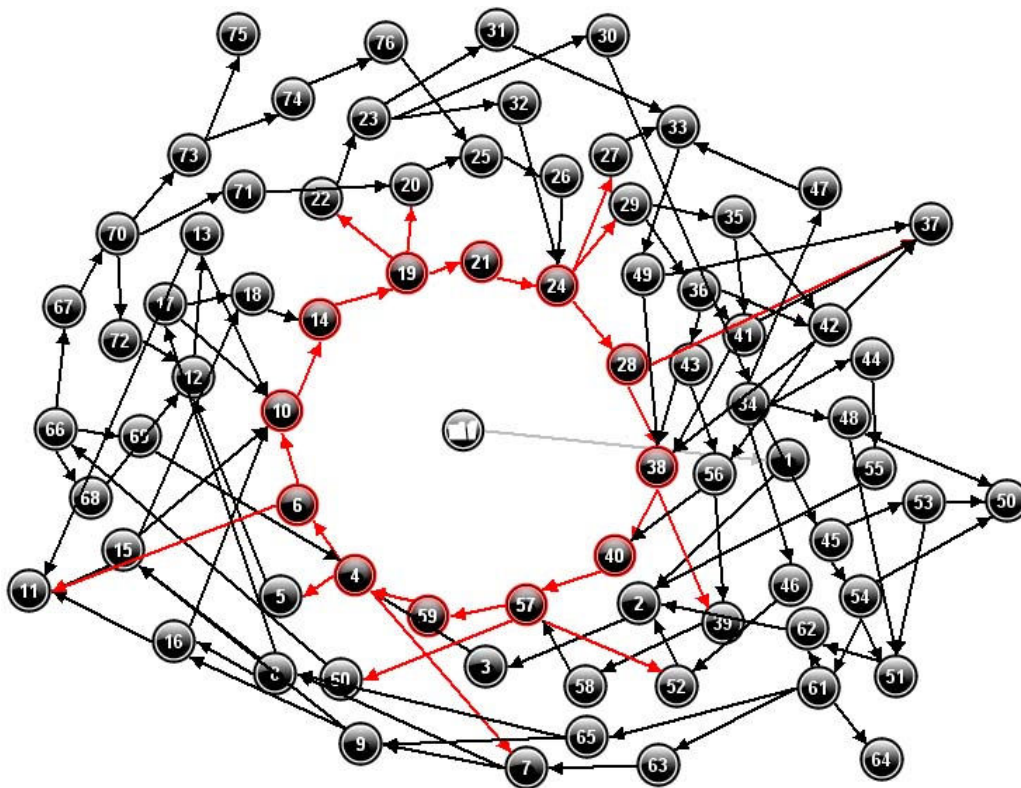


Figure 6.15: 1. The complete state-graph of Scenario 1 with selected cyclic path {6, 10, 14, 19, 21, 24, 28, 38, 40, 57, 59, 4}

To inspect the behaviour shown in the selected path, the value history, as shown in Figure 6.16, is inspected. The first thing that stands out in the value history is that the value graph which describes the changes in Size of the deer lags behind but shows the same changes as the value graph which describes

the tree population reaches its minimum Size and Growth. In state 64, both the Growth rates stabilize and in state 11, both Growth rates reach their maximum.

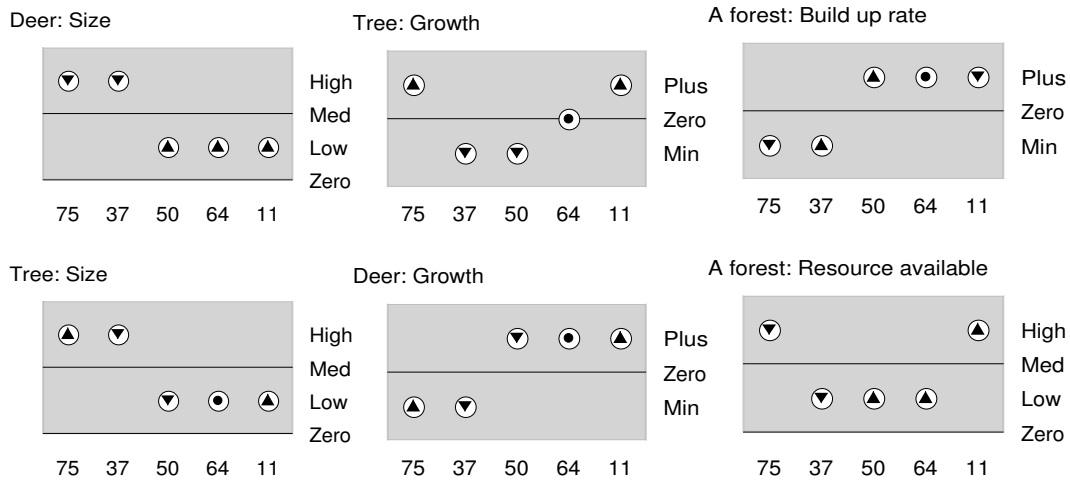


Figure 6.18: The value history of all the end states.

The causal model

The causal model in state 21 of the selected path is shown in Figure 6.19. It matches the implemented model fragments accurately with the adaptations made to the Single population model.

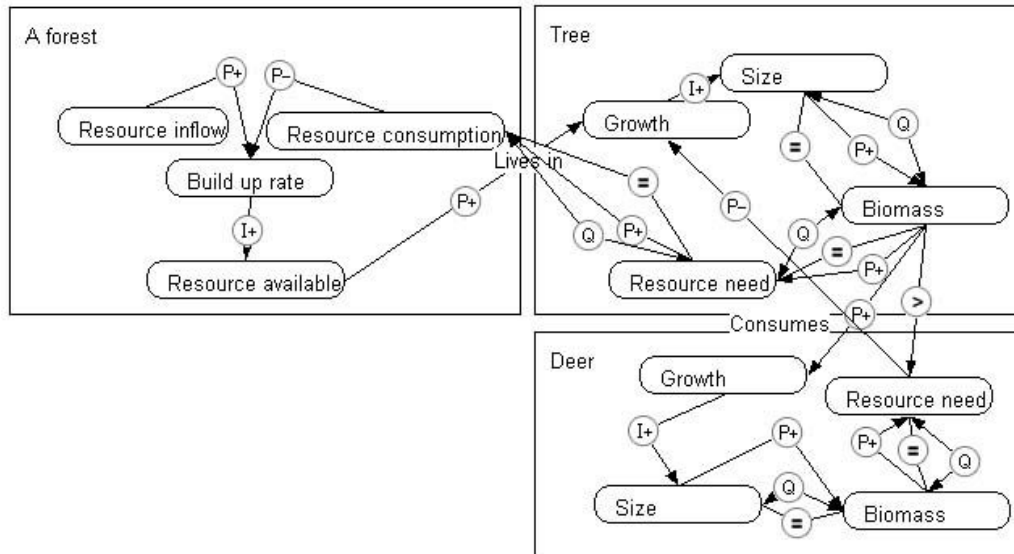


Figure 6.19: The dependencies in state 21.

6.3 Summary

In this chapter the dynamics of the Single population are adapted to a model which exhibits less ambiguity when simulated. This model is used in a predator prey interaction and tested in simulation. The results reflect typical predictions derived from the theory.

7 Evaluation by experts

7.1 Introduction

This chapter describes the results of two interviews with domain experts. The domain experts that were consulted are active in the NaturNet-Redime project (<http://naturnet.org/>), which is concerned with capturing ecological knowledge in qualitative models.

The interview was set up as follows:

The experts were shown the causal model constructed in chapter 4 and an explanation was given. When the experts had any questions about the model, these questions were answered by using the explanations of the modelling choices described in chapter 4. When the causal model was understood, the experts were asked for their opinion on how well they thought this model represented the real world system it expressed.

Then the Single population model and its simulation results were shown and an explanation was given of the model fragments. The results of the simulation were explained using the inspection tools that Garp3 offers. After all was discussed, the experts were asked to give their opinion on how well the qualitative model reflected the principles derived from the theory and whether the results match the real world situation.

7.2 Interview with expert 1

7.2.1. The causal model

Some questions and remarks expert 1 had about the Causal model:

1. What about available space in relation to the other kind of resources?

The expert comments that from the conceptual point of view, there is a relationship between the nutrients, water and energy and available space. When the space is limited, then the other resources are also limited, so there is a redundancy. He thinks it is acceptable to assume that, because of the relationships between space and water, space and nutrients and space and energy, these resources can be modelled in one quantity in the qualitative model. Available space is an indirect way of measuring the resources and because of the redundancy, available space and density can be left out of the qualitative model.

2. The usage of per capita birth- and death rates. What is the reason to use this idea of per capita?

As explained in the modelling choices the per capita rates are used because they represent averages and thus there will be no influence from Size towards the rates. So the per capita birth- and death rates will remain steady when the Size changes. This reduces complexity.

The expert comments that the per capita rates cannot easily be changed, so this notion of the per capita birth- and death rate changing under influence of resource shortage or abundance is incorrect, because it is an average over a long period of time and it will not change when there is starvation. When a part of the population dies, the resulting smaller population will still have the same per capita rates as the bigger population, because per capita is an average value. The actual number of birth and deaths of the population change when the size of the population changes, but the per capita rates change only when for example birth control is exerted.

He argues that the explanation given about why the per capita birth- and death rates are used is not clear enough to explain why the per capita rates are used instead of the normal birth- and death rates.

3. Why is the per capita birth and death used, but not the per capita immigration and emigration rates?

The expert comments that immigration and emigration rates have to be expressed in the same way as the birth and death rates. There is also a relation between emigration and size, as you have to take into account the size of the population when looking at emigration. When the per capita birth and death are used, it is necessary to express immigration and emigration also in per capita to make it possible to compare their influences.

4. *Why are all the resources put together in one quantity? Water is matter, nutrients are matter but sunlight is energy, is there no conflict when seeing these all as one?*

There is some discussion but no disagreement that all organisms need sunlight direct or indirectly, and because of that all organisms need the plants which are the primary producers. The plants transform matter into matter, and energy into energy. Organic matter produced by the plant is the energy plus the material they took from the environment. Other populations feeding on plants use the energy from the sunlight and matter from the environment stored in the plants.

5. *Why are the Size, Biomass and Resource need, which are different things, considered to change in a similar way?*

Size represents the number of individuals, Biomass represents the mass of all the living matter of the population and resource need represents the energy need of the population. They are not the same, but they are related. In the causal model it is only expressed that when Size increases, the Biomass also increases, which is correct.

In a model, normally, it is tried to use only one of these things, like in the R-star model, which only uses Biomass. Its not incorrect to model it like this, but there should be a note in the report. The expert also comments that sometimes individuals cannot be counted, or one individual is very large. When trees grow, the number of individuals remains the same, but the biomass increases. Larger trees do not necessarily need more resources, because they consist of mostly dead matter.

Opinion of the expert

Question: How does the causal model represent the ecological principles of the single population growing in an environment? Is it a valid representation of the real situation?

Answer: The expert thinks that the causal model is a valid representation of the real situation, although it is not completely clear on the point of per capita representation.

7.2.2. The qualitative model: the Single population model

Some questions and remarks:

The expert asks whether there is a scenario where only the mechanism of regulatory processes is shown, but it is not possible to create such a scenario because Fulfilment_rate will not get a value without the environment so there is no simulation of only that part of the model.

The expert comments that it is acceptable to assume the equality between the Resource_need of the population and the Resource_available of the environment.

The expert asks if there is an agent in the model. He says the Immigration could be described as an agent. But Emigration is no agent, because this is set by the population itself. It could be a modeling choice to model the process of immigration as an agent, but it is not incorrect as it is.

Opinion of the expert

Question: Does the behaviour shown in the simulation represent the behaviour of a single population growing in an environment correctly?

Answer: The expert thinks the Single population model it is a good representation of the real situation and the behaviour is correct.

The expert has some final remarks on the potential use for the model:

He wishes to know what the goal of this model is and who could use the model. Not only would this model be useful for prediction tasks about populations living in environments, but also to give a representation of concepts or trying to change the way of thinking about this system and therefore the behaviour. Most ecologists know this system, but in this model they can make changes and see what happens to improve their understanding of the system. Particularly, the discussion of the causal model is very insightful for researchers, for students and for managers.

Having this causal model, we can build a model with some different aspects, this would add to our understanding of the concepts. Also, this understanding is expressed in a formal way, which is a very

nice feature. He suggests starting the thesis with a discussion of how this model may aid the understanding of the problem.

7.3 Interview with expert 2

7.3.1 The causal model

Some questions and remarks expert 2 had about the causal model:

1. Why are the per capita rates used?

As explained in the modelling choices, the per capita rates are used because they represent averages and thus there will be no influence from Size towards the rates. So the per capita birth- and death rates will remain steady when the Size changes. This reduces complexity.

The expert explains that the situation, according to him, is as follows: The gross birth and death rates (the number of births and deaths) reflect the actual numbers of births and deaths while capita give more of a probability to die or reproduce; an estimate. The influence of resources takes place on an individual level in the population, and thus influences the capita rates, because these are calculated per individual, and via the capita rates, the gross rates are calculated by multiplying with the population size. Then size has an influence on both the gross birth- and death rates, which change in the same way as size does. The choice for per capita rates is not necessarily good or bad, but needs to be explained in the report.

However, the expert thinks that per capita rates can be influenced by occurrences of starvation. The growth rate which is a calculation of the births minus the deaths changes under influence of the available resources. However there are two equations in the theory about the situation of growth: (1) The logistic model and (2) the mechanistic model. In the logistic model ecologists define carrying capacity, which according to the expert is not fully explained. In the mechanistic model the resources directly influence the growth rate and supply an explanation for the changes in growth rate. The expert disagrees with the logistic model.

When looking closer, the expert says that in the causal model, the gross rates should probably be put in, because part of the per capita effect is already taking place in the calculation of the fulfilment rate. Per capita rates take a more individual perspective, and is also a notion of the quality of life, which is also hidden in the fulfilment rate. Including the per capita rates in the causal model is not wrong, but needs an explanation.

2. Why are the different kinds of resources seen together as one quantity?

The expert comments that there is a theory which states that the population is limited by the most limited of resources, which validates taking all the resources together in one quantity.

3. Why are density and available space left out of the qualitative model?

The expert also comments that density and available space are aspects of the logistic model and thus, when properly explained why they are left out, it is valid to leave them out.

Opinion of the expert

Question: How does the causal model represent the ecological principles of the single population growing in an environment? Is it a valid representation of the real situation?

Answer: The expert thinks that the causal model is a valid representation of the real world situation and the theory, given the explanation provided during the interview.

7.3.2 The qualitative model: the Single population model

Some questions and remarks:

Some things are left out of the causal model, and are not implemented in the qualitative model. There should be an explanation for ignoring some of the things left out of the model although they are redundant.

The expert comments that the idea of fulfilment rate is perhaps interesting to use in his further research.

He wonders whether there are simulations with every resource modelled in a separate quantity. It would be interesting because the theory that the population is limited by the most limited of resources could be illustrated by such a simulation. Such a simulation is not yet made in the Single population model and would raise the probability of ambiguity in the simulation result.

Opinion of the expert

Question: Does the behaviour shown in the simulation represent the behaviour of a single population growing in an environment correctly?

Answer: The expert thinks that the behaviour shown is an accurate reflection of the real situation. It is not observed in nature that plants show cycling behaviour. However, the expert believes they could do, the fluctuations being so small that it is not measurable. The behaviour never stabilizes in Medium, but that is also an accurate representation of what is going on, because there is no absolute stable situation.

7.4 Summary

Both experts agree that the causal model represents the ecological principles of the single population growing in an environment and that it is a valid representation of the real situation. The notion of using per capita or gross birth- and death rates raised questions for both experts however.

Both experts agree that the behaviour shown in the simulation represents the behaviour of a single population growing in an environment correctly.

8 Conclusions and discussion

8.1 Conclusions

This thesis describes a qualitative modelling effort in the field of population dynamics. A prerequisite of this modelling task was that the resulting model parts adequately represent the ecological phenomena, are compact, and reusable in larger models. Based on an extensive literature review a causal model of population behaviour has been developed and is described in this thesis. The causal model forms the basis of the implementation of the phenomena in Garp3. This modelling task was executed according to the steps formulated in the methodology framework developed in the NatureNet-Redime project. To test the implemented model, several scenarios have been created that implement simulations of specific situations in which different versions of the single population behaviour are involved. The results are successfully validated, based on comparison to the behavioural predictions derived from ecology theory. The developed model is also compared with a model which takes an alternative approach to the problem, the R-star model. It turns out that although there are several differences in approach and implementation, both models have a lot in common. To test the reusability of the Single population model parts, they are reused in a bigger model describing a predator-prey interaction between two populations. In order to do this, the dynamics of the Single population are adapted in order to exhibit less ambiguity when simulated. This model is tested in simulation and reflects typical predictions derived from the theory. The final evaluation step, records the opinion of two experts who were questioned about the model and the simulation output. From the obtained results and evaluation, it can be concluded that the Single population model developed in this thesis, is a valid and conceptually correct representation of the real world situation of population dynamics and that it captures the basic principles underlying the theory. However, the reusability aspect of the model parts requires further study.

8.2 Discussion

The domain of population and community dynamics is vast and complex, and perhaps too complex to be captured and create adequate understanding of the principles in such a short period of time. The basic knowledge about the principles was difficult to obtain, and even after the review was done and it was decided that sufficient knowledge of the concepts in the domain was derived, things turned out to be unclear. From the discussion with the domain experts it became apparent that ecologists not always agree upon the meaning and working of their concepts. When doing future research on this topic, it is recommended to involve more domain experts in the orientation phase of the modelling effort.

When discussing the causal model, both experts concluded that the issue of per capita or gross birth- and death rates should have been explained better. It is not enough to decide which concept to use on the notion of reducing complexity, although it may be a logical choice for a model builder. After thoroughly discussing the concept with both domain experts it was decided that for the qualitative model it makes no difference whether the gross or the per capita birth- and death rates are used. When using the gross rates, there should be feedback from the rates to the size or biomass of the population, but since this feedback is of equal magnitude for both rates, it does not influence the equality relation between the births and deaths, which is the most important fact when calculating the growth rate. However, when choosing one of the two representations, gross or per capita, the immigration and emigration rates should also be represented in the same way.

Another discussion concerns the reusability of the Single population model. When reusing the model in the Predation model, it had to be adapted in such a way that only the principles underlying the model remained untouched. The question remains whether the model is truly reusable. It is reusable in such a way that it is applicable on any population of species, but from the results obtained in this thesis, it can not be concluded that the model is also reusable in models that contain multiple populations of species.

Also, the results obtained in chapter 6 are insufficient to conclude whether the Predation model actually shows the behaviour derived from the theory. When looking at the model results, it can be observed that the behaviour of the selected behavioural path is similar to the behaviour shown by the producer population without the introduced predator. This could mean bottom-up control by the prey, but it can

also mean that the influence from the predator on the prey was implemented inadequately. All in all, there is uncertainty about the correctness of the results and therefore no solid conclusions can be drawn other than that the results are promising and that future research should be done to develop more conclusive models about predator-prey interactions.

8.3 Future work

A logical step following from the work presented in this thesis would be to develop a model that includes more than two populations. The literature describes several examples in which multiple populations interact (Campbell & Reese, 2002).

Also, with the uncertainty about the correctness of the predation model, another possibility following from this work would be to develop a predation model which retains the Single population dynamics, especially including birth- and death rates, instead of using the growth rate, which still results in an insightful behavioural graph.

Looking into another direction, it would be interesting to research whether the presented models would indeed be useful in ecology education or to start discussions among ecologists about the meaning of ecological concepts and whether qualitative models that can be simulated on a computer would add to their understanding of the problem.

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Appendix A: Glossary of ecology terminology

Abiotic	Non-living chemical and physical factors of the environment (e.g. light, water, temperature, etc.)(Campbell & Reece, 2002)
Biomass	Total mass of living organisms within a specified area.
Biotic	The living components of the environment, such as plants, animals and fungi, that affect ecological functions, as opposed to abiotic (Strange days glossary).
Boom or bust	Some populations go through periods of low population growth, then more exponential growth, and then a dying out period. These fluctuations in population growth can cycle due to food limitations, predation or other factors (Campbell & Reece, 2002).
Carrying capacity	The maximum number of organisms that can use a given area of habitat without degrading the habitat and without causing social stresses that result in the population being reduced (Strange days glossary).
Community	All species or populations living together in the same area, usually interacting or depending on each other for existence(Campbell & Reece, 2002).
Convection	Is the vertical air circulation in which warm air rises and cool air sinks, resulting in vertical transport and mixing of atmospheric properties. It is also the flow of heat by this circulation (Mountain Meteorology: Fundamentals and Applications).
Demography	Abiotic and biotic factors that affect population growth. (Campbell & Reece, 2002)
Dispersal	The permanent emigration of individuals from a population to a new area.
Ecosystem	The natural system in which energy and nutrients cycle between plants, animals and their environment.
Environment	The complex of physical, chemical, and biological factors in which a living organism or community exists.
Foraging	Behaviour associated with obtaining or consuming food.
Habitat	The area or environment where an organism or ecological community normally lives or occurs.
Nutrients	Substances which are required to support living plants and organisms. Major nutrients are carbon, hydrogen, oxygen, sulphur, nitrogen and phosphorus.
Organism	A living being.
Population	A group of individuals of the same species which are capable of interacting with each other in a localised area.
Species	A group of organisms that have a unique set of characteristics (like body shape and behaviour) that distinguishes them from other organisms. Individuals within the same species can typically reproduce with each other to produce fertile offspring. Species is the basic unit of biological classification (Strange days glossary).
Taxonomic	The classification of organisms in to categories based on common characteristics.

Appendix B: Modelling primitives

Building Blocks

There are some static building blocks that underlie each qualitative model. These do not represent behaviour, but are used to define the structure of the system and can be manipulated by the dependencies described later on.

Entities

An entity is an important physical object in the system that is being modelled but it can also be an abstract concept that is important within the system. Entities are structured in the entity hierarchy, which is a subtype taxonomy. Subtypes inherit all the properties of the parent type they descend from, plus some added new ones which distinguish them from the other subtypes. Subtypes can also be the parent for new subtypes.

Agents

Agents are those model elements that represent external factors in the system. Like entities agents are structured in a hierarchy.

Configurations

A configuration is a relation between instances of entities and agents. Configurations connect entities and agents so structures can be defined. Configurations are also called *structural relations*.

Attributes

Attributes are static properties of entities. They can be used to describe certain aspects of entities that do not change while the system is active.

Quantities

Quantities are properties of entities that do change. They can be used to describe aspects of entities that can have multiple possible values and which can be influenced directly or indirectly by other aspects of the system. Quantities have quantity values.

Qualitative value

A qualitative value can be a point or interval. A point value defines an important landmark of the system while an interval describes a value more loosely.

Quantity space

A quantity space consists out of several qualitative values. Most quantity spaces have the point value zero, to describe a point where for example the height of the water level is zero. An example quantity space is {Plus, zero, Min}, where plus and min are interval values and zero is a point value. Zero can also describe a turning point between positive and negative values. (This is important because values are labels).

Magnitude

The current value of a quantity as described in the quantity space is called the magnitude.

Derivative

The derivative is part of the quantity value and describes the changes of the quantity. It can be min (decreasing), zero (steady) and plus (increasing).

Quantity value

The quantity value is a combination/set of two parts, the value of the magnitude and the value of the derivative.

Assumptions

An assumption is a label of a condition that needs to hold for a model fragment to fire. The label describes the condition, but the model builder needs to add the condition in a scenario to make it fire in the simulation. Assumptions are a tool to restrict the possible behaviours of model fragments and assure that some model fragments only fire under certain conditions.

Dependencies

Dependencies are those elements of the model structure that cause behaviour. They can change quantity values directly or indirectly and connect quantities through causal relations.

Influences

Processes are modelled by influences, directed relationships between quantities. Influences can be positive or negative. The source magnitude and the type of influence determine whether the derivative of the target quantity increases or decreases. $I+(B, A)$ means that there is a flow A that causes B to increase when A has a positive magnitude and decrease when A has negative magnitude. $I-(B, A)$ means that there is a flow A , that causes B to decrease when A has a positive magnitude and increase when A has a negative magnitude.

Proportionalities

Proportionalities model the indirect effects of processes. They propagate the effects of a process and set the derivative rather than the magnitude of the target quantity. Proportionalities can also be positive or negative. $P+(B, A)$ means that changes in A , in a particular direction cause B to change in the same direction. $P-(B, A)$ means that changes in A , in a particular direction, cause B to change in the opposite direction.

Inequalities

Inequalities are ordinal relations expressing equalities and inequalities between quantity/qualitative values in the system. Inequalities can be $<$, \leq , $=$, \geq , and $>$. There are several possible ways to use inequalities, due to the possibility to connect them to magnitudes, points of magnitudes, derivatives, zero point of a derivative and plus/min relations. Inequalities are always created between points, it is not possible to define them for intervals. It can be said that a magnitude is greater than zero for example, but not that zero is greater than a magnitude. That makes eleven possibilities in total.

Value

Values are equality expressions to assign a static value to a magnitude or derivative. Assigning a value to a derivative will create quantities that will not change at all or will only increase or decrease. Assigning a value to a magnitude will set the magnitude to that specific value. Unlike inequalities, values can be used on intervals.

Plus/min

With plus/min relations differences and sums of magnitudes, points in the quantity space of a magnitude and derivatives can be calculated. Plus/min relations can be the target or the source of inequality relations. They can also be connected to other plus/min relations or be connected by several inequalities.

Correspondences

Correspondences are means to reduce ambiguity by indicating that values in quantity spaces react in the same way to changes and thus have the same qualitative values. Correspondences can be directed or undirected, meaning that respectively the target value changes when the source value changes or it works both ways. There are three types of correspondences.

Value correspondences are relations between qualitative values of quantity spaces of different quantities. Depending on the fact if the correspondence is directed or undirected, a *quantity space correspondence* indicates that all of the values in the quantity space of the target correspond to all the values in the quantity space of the source. This kind of correspondence can also be inversed, corresponds the last value

of one quantity space to the first value of the other quantity space and so forth. The final type of correspondence is the *full quantity space correspondence*. This type creates a quantity space correspondence between both the magnitudes and the derivatives.

Model Fragments

A model of a system consists of many parts working together. Model fragments are those parts which are created out of building blocks and dependencies by the model builder. Model fragments are rule based and every ingredient added to the fragment is either a condition or a consequence.

Conditions and Consequences

Conditions are those model ingredients that have to be true in order for the model fragment to be added to the scenario by the simulator and the consequences to be executed as facts about the system's behaviour. Consequences are those ingredients of a model that are added to the simulation structure when the conditions of the model fragment are met. In Garp3, conditional model elements are red and consequence model elements are blue.

Static

Static model fragments are those structures of model ingredients that do not contain influences and agents. Their purpose is to describe the basic structure of the system including the proportionalities that exist between quantities.

Process

Process fragments are those structures that do contain direct influences but not agents. The purpose of these model fragments is describe the processes that take place in the system.

Agent

Agents fragments are used to describe structures of the model that contain agents and are outside of the system. Agent fragments can contain one or more influences and describe the influences external factors have on the system.

Scenario

A scenario is a description of a specific situation, stating the conditions which are true at the beginning of the simulation. Ingredients added in a scenario must be matched by model fragments. Consequences can be added to the system structure when the simulator can match the conditions of one or several model fragments to those stated in the scenario. These consequences can start processes which in their turn can lead to multiple connected states from which behaviour can be derived.

Appendix C: Model fragments of the Single population

In this appendix several model fragments of the Single population are shown that were left out of chapter 4. Several inequality conditions are added as static model fragments. These model fragments force the reasoning engine to consider all possible equality relations between two quantities.

Inequalities between Per_capita_birth and Per_capita_death:

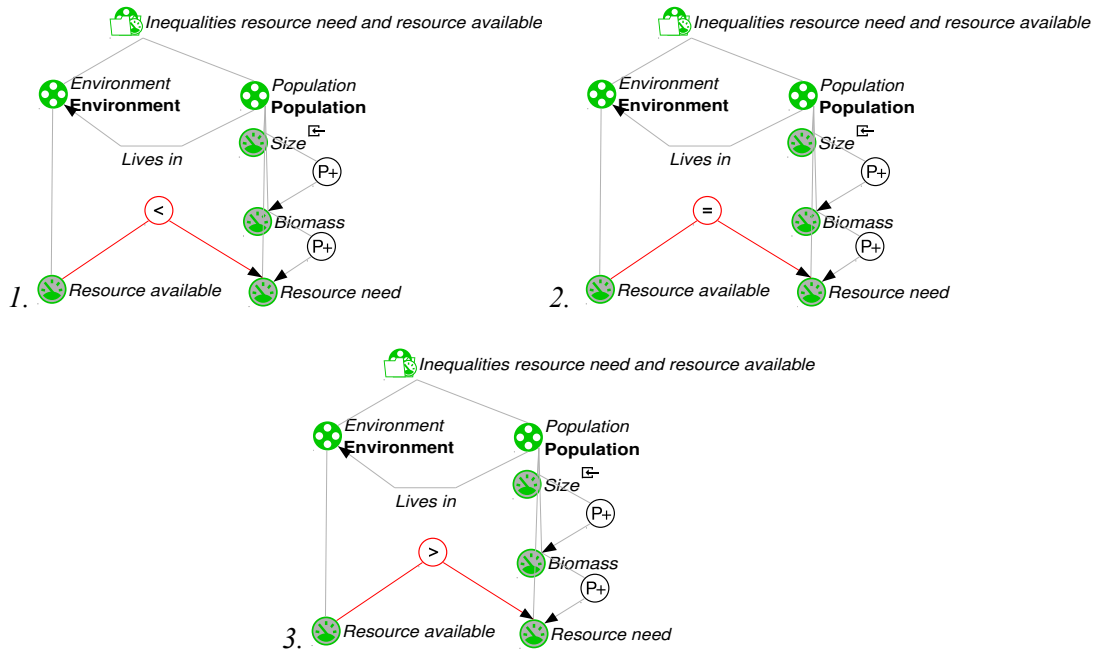


Figure C.1: All inequality conditions between birth and death, descended from the model fragment *Inequalities birth and death*.

Inequalities between Resource_need and Resource_available:

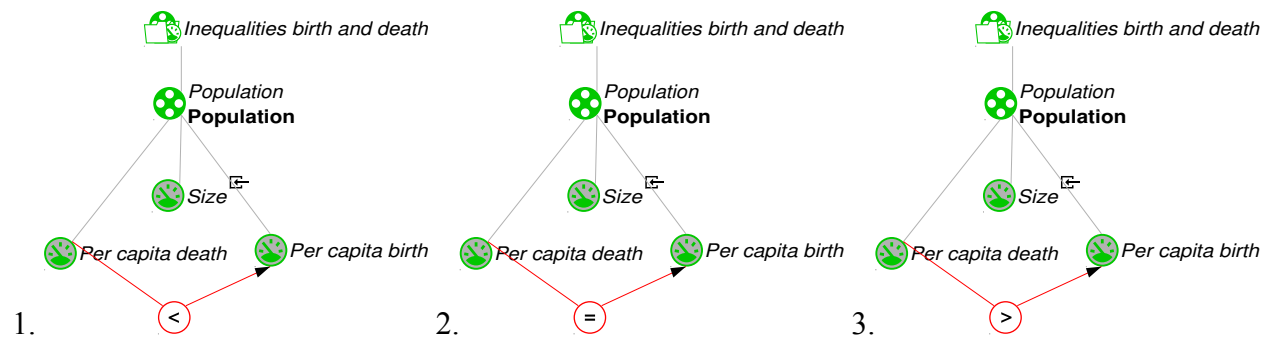


Figure C.2: All inequality conditions between Resource_need and Resource_available, descended from the model fragment *Inequalities resource need and resource available*.

Appendix D: Model fragments of the R-star model

In this appendix several model fragments of R-star model are shown that were left out of chapter 5.

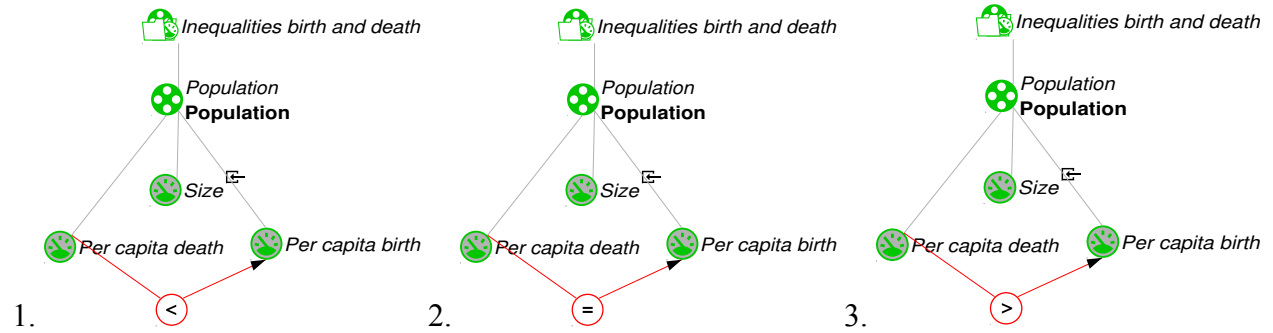


Figure D.1: Inequalities between Resource_inflow and Resource_consumption

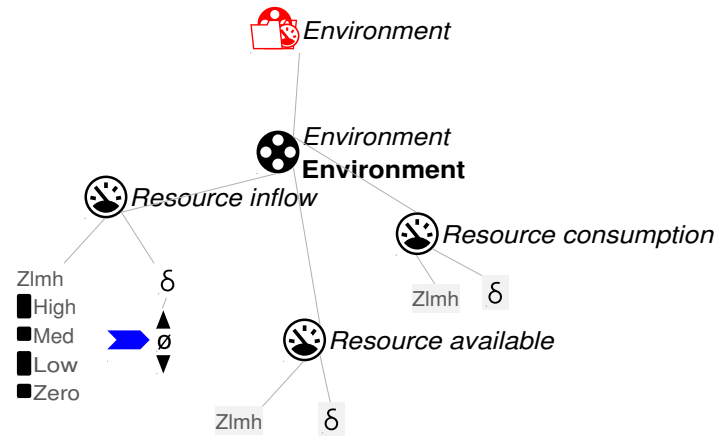


Figure D.2: The Assume constant resource inflow fragment

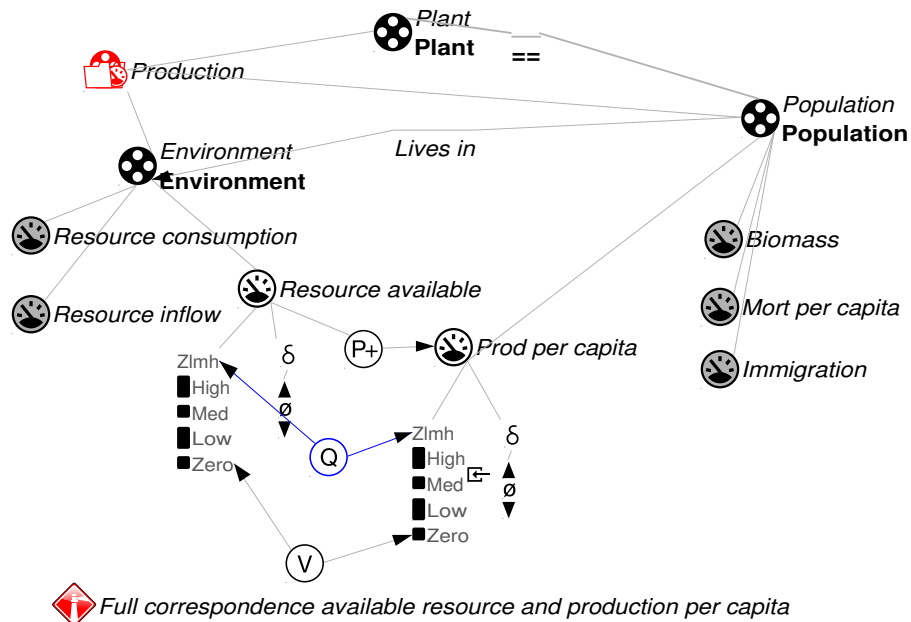
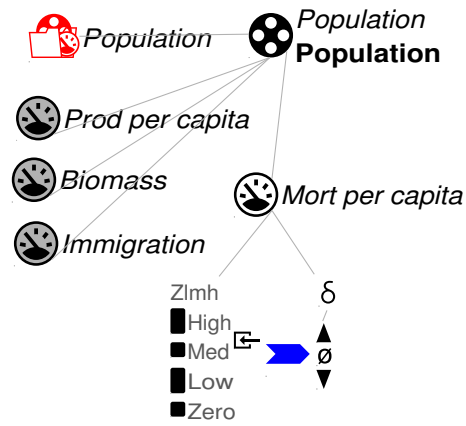
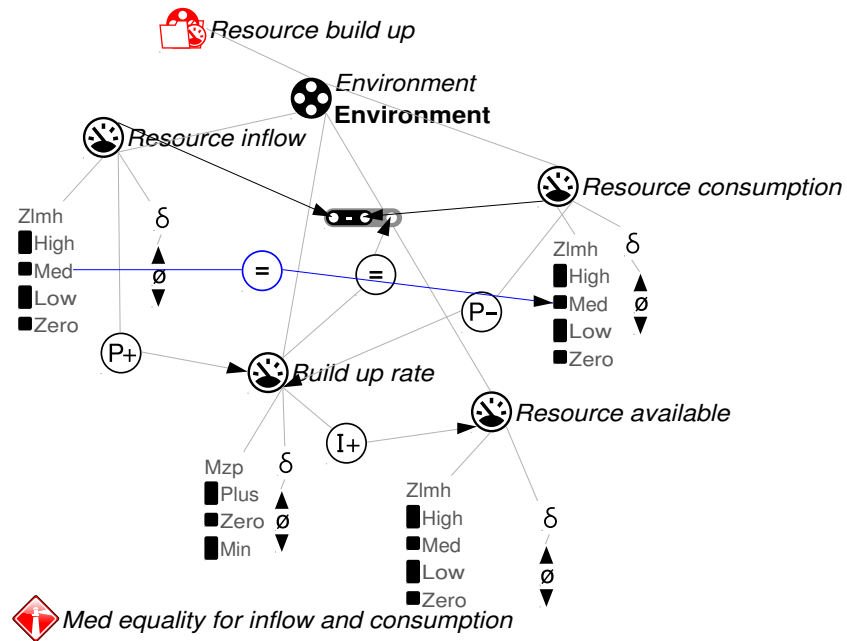


Figure D.3: Assume full corresp available resource and prod per capita model fragment

Figure D.4: The *Assume constant mort per capita* model fragmentFigure D.5: The *Assume inflow consumption equal med value* fragment

Appendix E: Model fragments of the Predation model

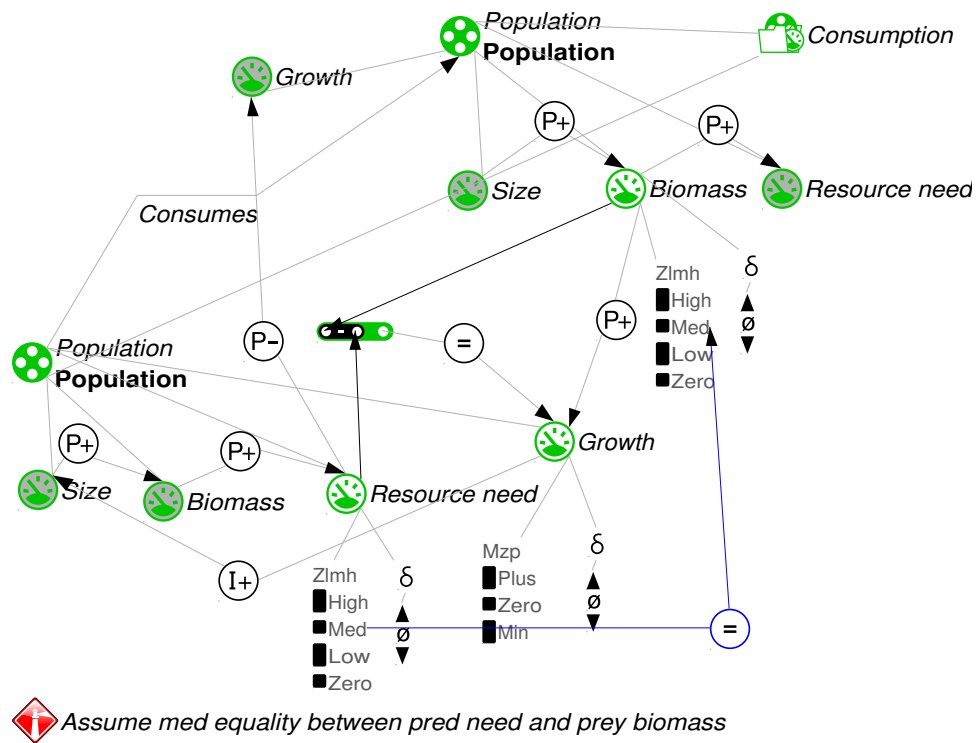


Figure E.1: The Assume med equality between pred need and prey biomass model fragment.

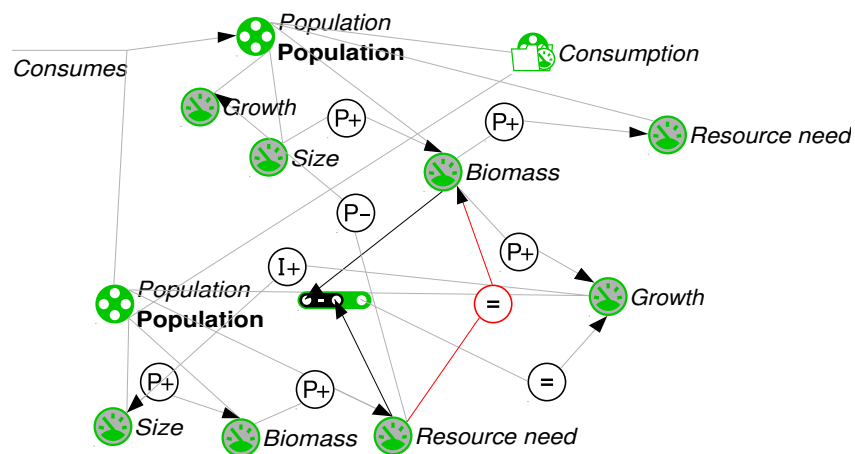


Figure E.2: The *Biomass eq resource need* model fragment.