Qualitative Reasoning about Population and Community Ecology

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■ Traditional approaches to ecological modeling, based on mathematical equations, are hampered by the qualitative nature of ecological knowledge. In this article, we demonstrate that qualitative reasoning provides alternative and productive ways for ecologists to develop, organize, and implement models. We present a qualitative theory of population dynamics and use this theory to capture and simulate commonsense theories about population and community ecology. Advantages of this approach include the possibility of deriving relevant conclusions about ecological systems without numeric data; a compositional approach that enables the reusability of models representing partial behavior; the use of a rich vocabulary describing objects, situations, relations, and mechanisms of change; and the capability to provide causal interpretations of system behavior.

Why use qualitative representations for ecology? A number of textbooks published recently (for example, Haefner [1996]; Jørgensen and Bendoricchio [2001]) show that ecological modeling is almost synonymous with mathematical model building. These models might be precise and sometimes closely mimic what we believe is happening in the field, but they often fail to capture the mechanisms that actually explain the observed behavior (Gillman and Hails 1997). Moreover, they require numeric data of good quality, and ecological data are often difficult to obtain because long-term observations are required, and experimentation with real systems is limited. Hence, ecological knowledge is heterogeneous, including both quantitative and qualitative aspects. It is imprecise, incomplete, qualitative, and fuzzy; is expressed verbally and diagrammatically; and is, therefore difficult to model using a mathematical approach. As noted by Rykiel (1989), ecologists have a considerable amount of knowledge "in their heads" and not many ways to make this knowledge explicit, well organized, and computer processible. In this article, we show how qualitative models can be used to address some of these problems and, thus, become a valuable complement for mathematical approaches to ecological modeling. After all, many questions of interest in ecology (especially to decision makers) can be answered in terms of "better or worse," "more or less," "sooner or later," and so on (Rykiel 1989).

Qualitative representations provide a rich vocabulary for describing objects, situations, relations, causality, and mechanisms of change (for example, de Kleer and Brown [1984]; Forbus [1984]). With this vocabulary, it is possible to capture commonsense knowledge about ecological systems and use this knowledge to automatically derive relevant conclusions without requiring any numeric data. Another important feature concerns the idea of using a compositional approach to enable reusability (Falkenhainer and Forbus 1991), which is achieved by constructing libraries of partial-behavior descriptions that apply to the smallest entities relevant within a domain. As larger systems are built from these basic elements,

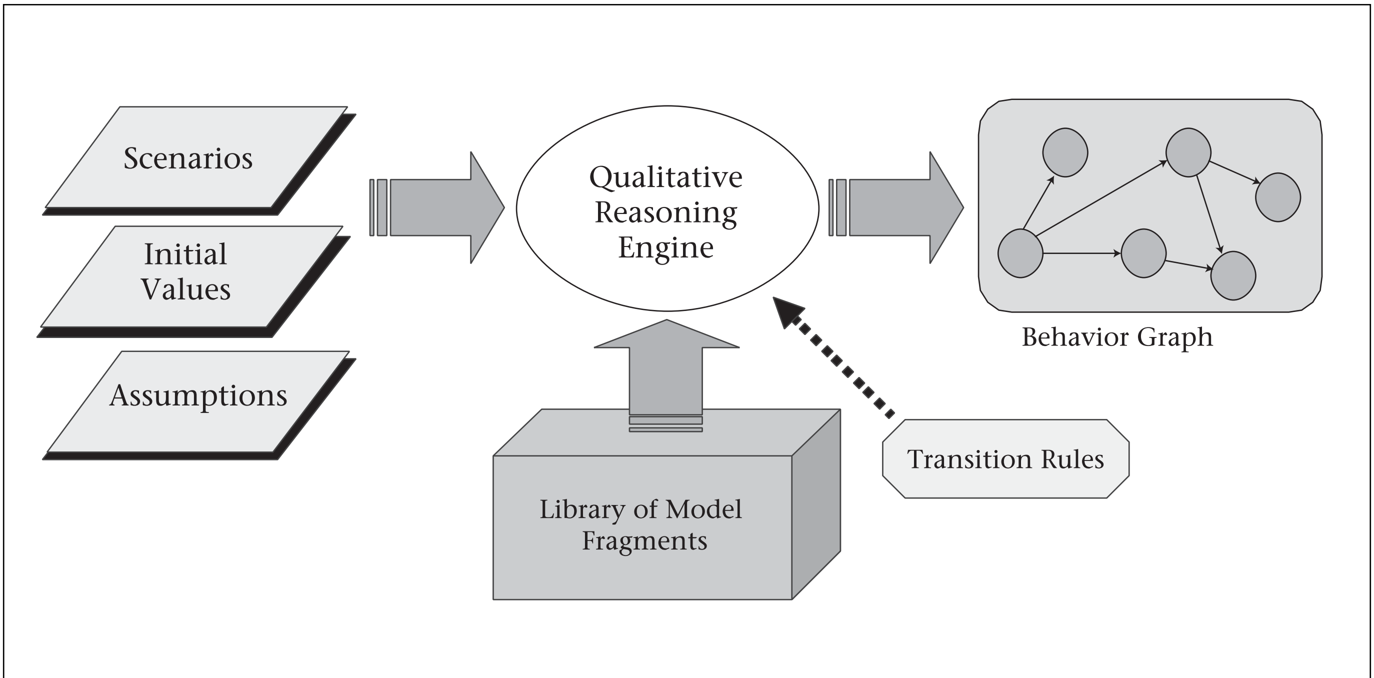

Figure 1. Basic Architecture of the Qualitative Reasoning Engine.

reasoning about the behavior of larger systems means combining the behavior of these elements. Thus, we avoid having to develop dedicated models for each system encountered. A third feature of qualitative models, relevant to ecological modeling, is their ability to provide causal explanations of system behavior. Deriving the behavior of a complete system from the behavior of its constituents facilitates an explanation of the overall behavior in terms of these constituents. Such explanations are considered insightful, particularly when the set of partial models captures a causal account for the behavior of the constituents (for example, Forbus [1988]).

An interesting problem to illustrate the potential of qualitative reasoning for modeling ecological knowledge comes from the Brazilian cerrado vegetation. The cerrado is a large biome consisting of a number of different physiognomies (well-defined communities). According to a widely accepted hypothesis, changes in the fire frequency influence the composition of the cerrado vegetation. This succession hypothesis states that bio-diversity is lost, and the vegetation becomes dominated by grass species when the fire frequency increases. When the frequency decreases, the vegetation changes into forestlike physiognomies. The hypothesis has received support from different studies (for example, Coutinho [1990] and Moreira [1992]) and become the basis for environmental education and management decisions about the cerrado. However, knowledge about succession in the cerrado is incomplete and imprecise. It mainly provides a conceptual description of the succession process. Our goal is to construct models and run simulations that express this conceptual knowledge.

In the following section, we first introduce our qualitative theory of population dynamics. The implementation of this theory results in a library of partial models. With this library, simulations can be created that explain the behavior of populations in terms of the basic processes that determine it. We then use this library to construct models and generate simulations of typical interaction types between two populations. Finally, we augment the library with knowledge about the cerrado physiognomies and how they are influenced by environmental factors. The same qualitative theory of population dynamics is then used to create simulations of community dynamics, particularly on how changes in the fire frequency influence the behavior of the cerrado vegetation. The article closes with a brief discussion of related work.

A Qualitative Approach to Population Dynamics

In this section, we introduce qualitative models of the basic processes that govern the behavior of populations. The models are imple-

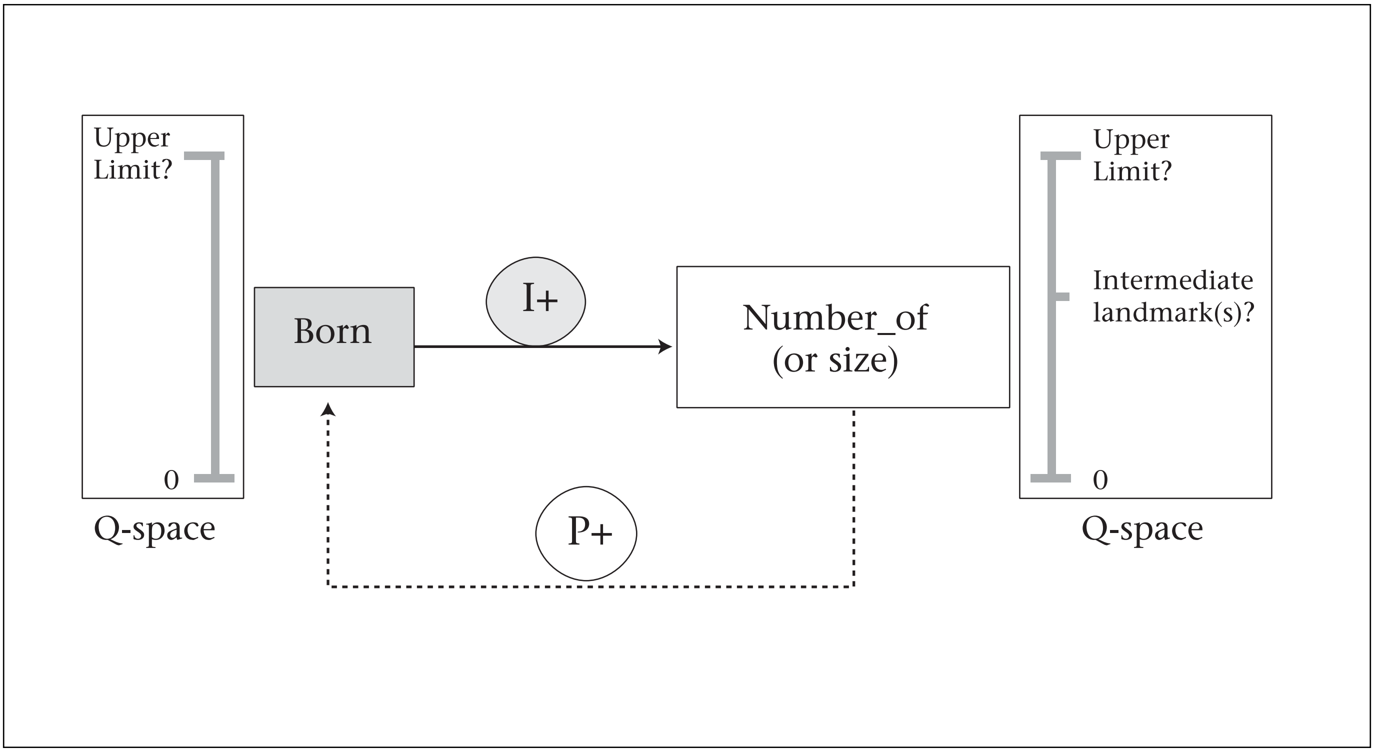

Figure 2. Causal Dependencies Capturing Natality as a Basic Process.

mented in GARP (Bredeweg 1992),[1] a reasoning engine that takes a compositional modeling approach (Falkenhainer and Forbus 1991) to qualitative modeling. The reasoning engine works on the basis of three main constructs: (1) scenarios, (2) model fragments, and (3) transition rules (figure 1). Scenarios specify initial situations for the simulator to start behavior prediction. Model fragments capture knowledge about the behavior of system parts and are used to assemble states of behavior. Assumptions can be used to further detail the applicability of a model fragment. Transition rules determine valid transitions between states of behavior. After selecting a scenario, the engine proceeds with the prediction task by recursively consulting the library for applicable model fragments. This search is exhaustive, and each consistent subset of model fragments represents a behavior interpretation that matches the selected scenario.

Basic Processes

Based on the compositional modeling approach, an important goal is to construct model fragments that represent elementary behavioral units. To capture the insights that ecologists have concerning the behavior of populations, our starting point is the general growth equation typically found in ecology textbooks:

$$Nof(t + 1) = Nof(t) + (B + Im) - (D + E)$$

Here, *Nof* represents the number of individuals of the population at the beginning (t) and at the end of some time interval ($t + 1$). *B, D, Im, E* are birth, death, immigration, and emigration rates, respectively. Although there is great variability on how these four processes occur among animal and plant species, ultimately these are the only mechanisms that cause the number of individuals to change in any population. Notice that *B, D,* and *E* are functions of *Nof* and that the precise shape of these functions can vary according to the population type. Immigration (*Im*), however, seldom depends on the number of individuals already present in the population.

Now, how can we represent this conceptual knowledge on population ecology using a qualitative formalism? We start by applying the causal dependencies introduced by the qualitative process theory (Forbus 1984), notably positive and negative direct influences (*I*+, *I*–) and indirect influences (*P*+, *P*–) (an indirect influence is also referred to as a *proportionality*). Take, for example, natality. The flow of individuals being born is typically captured by an *I*+, meaning that “there is a flow *B* (birth rate) that causes *Nof* to increase”; thus, {*I*+(*Nof, B*)}. Next, given that the amount of individuals in reproductive activity is related to the population size, we can state that “changes in *Nof,* in a particular direction, cause flow *B* to change in the same direction." This is typically represented by an indirect influence: {*P*+(*B, Nof*)}. Figure 2 depicts this idea.

Following this approach, we can define four basic processes: (1) natality, (2) mortality, (3) immigration, and (4) emigration, each modeled by a separate model fragment. These model fragments include the following relations: {*I*+(*Nof, B*); *P*+(*B, Nof*)}, {*I*–(*Nof, D*); *P*+(*D, Nof*)}; {*I*+(*Nof, Im*)}, and {*I*–(*Nof, E*); *P*+(*E, Nof*)}, respectively. Notice that there is no indirect influence from *Nof* on *Im* because the immigration rate is modeled as independent of the population size.

Defining Quantity Spaces

An important aspect of a qualitative model concerns the values quantities can have: the *quantity spaces*. Quantity spaces in GARP consist of an ordered set of alternating points and intervals and are defined per quantity. A quantity space can include zero, which is universal for a model, meaning that all zeros are equal. Relationships between other values from different quantity spaces can be defined using (in)-equalities and correspondences. In each state of behavior, all quantity values are represented as magnitude-derivative pairs: <*mag, der*>. Most of the simulations presented in this article use a three-valued quantity space for the magnitude of *Nof: QS* = {zero, normal, max}, referring to the population does not exist, the population exists and has "some" size, and the population has reached its maximum size, respectively (see also later). Magnitudes of *B, D, Im,* and *E* are represented by the values zero and a positive interval, thus *QS* = {zero, plus}. Derivatives can take on values negative, zero, and positive, represented as *QS* = {–, 0, +}. Applied to the derivative of *Nof* and *B, D, Im,* and *E,* these symbols represent that the population and the rates are decreasing, stable, or increasing. For example, *Nof* = <normal, +> means that the state variable "number of individuals" has the qualitative value *normal* and is increasing.

Determining meaningful qualitative values for the magnitudes of quantities is a difficult task when building qualitative models about populations. Compare, for example, physics, where landmark values such as *melting* and *boiling points* define rather distinct substance behavior, involving different processes (Forbus 1984). There are not many obvious landmarks that uniquely characterize qualitative distinct behavior of an ecological system. Even *K*, the carrying capacity, as often used in population ecology, does not really relate to characteristic processes becoming active or inactive. To enforce a solution, we use the idea of *minimum required variation* (Salles and Bredeweg, 1997). That is, build quantity spaces such that they facilitate the generation of all the qualitative distinct states that are important for understanding the system at hand. Here, we want to capture the idea that there is a limit to the population growth; hence, an upper boundary (landmark) is required: *max*, although the real maximum value can change according to different circumstances. It should also be possible to express that a population is extinct or does not exist, hence, a specific lower boundary, namely, *zero*. Finally, the size of the population can be in between these extreme points, thus a positive interval immediately above zero to a certain maximum. We refer to this interval as *normal*. However, different perspectives might require a different range of values for *Nof*. For example, to characterize the different kinds of cerrado vegetation, it was necessary to divide the *normal* interval into three subvalues, *QS* = {zero, low, medium, high, max} (see the section entitled Communities and Environmental Factors).

Capturing Additional Knowledge

A flow of individuals, as, for example, modeled by the natality process, only occurs when a population exists. Therefore, a distinction must be made between situations in which a population exists and in which it does not. Two model fragments represent these situations: *Nof* > zero (there is a population), described in the fragment "existing population," and *Nof* = zero (there is no population), described in the fragment "nonexisting population." Processes natality, mortality, and emigration have the model fragment *existing population* as a condition and, thus, do not become active when the model fragment *nonexisting populations* is active. The ecological phenomenon known as *immigration* requires a special approach. Like the other processes, it can happen when the *existing population* fragment is active. We represent this knowledge as the *immigration process*. However, sometimes individuals of a population start to live in a new space, where the population does not yet exist, which is considered a special kind of immigration, the *colonization process*. The model fragment *nonexisting population* is conditional for the colonization process to become active.

A different perspective on population growth can be obtained by aggregating processes to get a single growth rate. As in most mathematical models, we define the *growth process* as a combination of the four basic processes, using the intermediate variables *Inflow* and *Outflow* to calculate the quantity *growth* rate. The qualitative growth equation then becomes an implementation of

Inflow = *B* + *Im*
Outflow = *D* + *E*
Growth = *Inflow* – *Outflow*

The overall population growth is modeled using a new model fragment, *population growth,* which also introduces the causal dependencies {*I*+(*Nof, Growth*) and *P*+(*Growth, Nof*)}. Different from the four basic processes, the growth rate requires the *QS* = {minus, zero, plus} to take care of situations in which Inflow is smaller, equal, or greater than Outflow.

When a quantity is simultaneously influenced by more than one direct or indirect influence, their effects are combined by influence resolution (Forbus 1984). In our case, *B* and *Im* rates are added, but *D* and *E* are subtracted from the derivative of *Nof.* The final result can be ambiguous, depending on the relative amounts of these four rates. Ambiguity is sometimes seen as a problem of qualitative models because the missing information can lead to enormous state graphs predicting a large number of possible behaviors.[2] We like to think of ambiguity as a feature, namely, one that drives the knowledge acquisition. When constructing a model, ambiguity can force the modeler to acquire additional knowledge to address the ambiguity, for example, by consulting experts. Sometimes this extra knowledge is unavailable, which can reflect a lack of understanding because of theoretical issues or point out the need for specific (empirical) research programs. In other situations, the simulation model produces a set of legal states the system can exhibit unless particular values are given to certain quantities. Here, *ambiguity* refers to possible behaviors of a system.

In a knowledge-sharing situation such as education, it is often helpful when the alternative trajectories of the system can be made insightful to the learner. This insightfulness can be realized using assumptions that implement relative magnitudes of quantities and, thus, reduce the ambiguity, making a simulation less complex. An interesting issue in this respect is the representation of migratory movements that either occur or do not occur, referred to as *open populations* versus *closed populations,* respectively. To capture this idea, two assumption labels are defined in our model: (1) open population and (2) closed population, which are used as conditions for certain model fragments. Particularly, the model fragment *assume closed-population* always applies when the closed-population assumption is true. It excludes migration by specifying that *Im* = *E* = *zero* and the derivatives $\delta Im = \delta E = 0$.

Simulating Single-Population Behavior

Now, that we have discussed the most important model ingredients, let us look at a simulation. Consider an initial scenario that introduces the objects *biological entity* and *population* and the quantities *Nof, B, D, Im, E, Inflow, Outflow,* and *Growth,* with no values assigned to them. It is assumed that the rates *B* and *D* are equal. Based on this scenario, the simulator produces eight initial states, with combinations of all the possible values for these quantities according to their quantity spaces and the constraints introduced by the applicable model fragments. These initial states are defined in terms of the state variable *Nof*: {<*zero*, 0>; <*zero,* + >; <*normal*, –>; <*normal*, 0>; <*normal,* + >; <*max*, –>; <*max,* 0>; <*max*, + >}. Further, simulating does not produce any new states because all possibilities have already been found, but it does generate all possible transitions between these eight states. Figure 3 shows the causal model representing the relationships between the quantities in state 3 and the value history diagram for *Nof* along the behavior path: {8 → 5 → 1 → 2 → 3 → 6}.[3] Black triangles and balls are used to represent the derivatives of the quantities.

Given the assumption that *B* equals *D,* all the behavior variation in this simulation originates from changes in the migratory behavior of the population. *Inflow* is bigger in states 2, 3, and 6 (the population grows), but *Outflow* is bigger in states 8 and 5 (the populations becomes extinct). In state 1, the population is nonexistent, and colonization takes place in state 2. The path depicted in figure 3 thus shows a maximum-sized population at the start that becomes extinct. After colonization, the population increases again to its maximum size.

Qualitative Models of Interactions between Two Populations

The previous section presented the basis for a qualitative domain theory of population dynamics. This section shows how this theory can be used to model typical interactions between populations. Relationships between two populations of different species can be classified either on the basis of the mechanism or on the effects of the interaction. Mechanisms of interaction take into account particularities of each species life cycle. If these details are left out and only the effects are considered, the interactions can be classified using combinations of the symbols {–, 0, + }. The change in a pop-

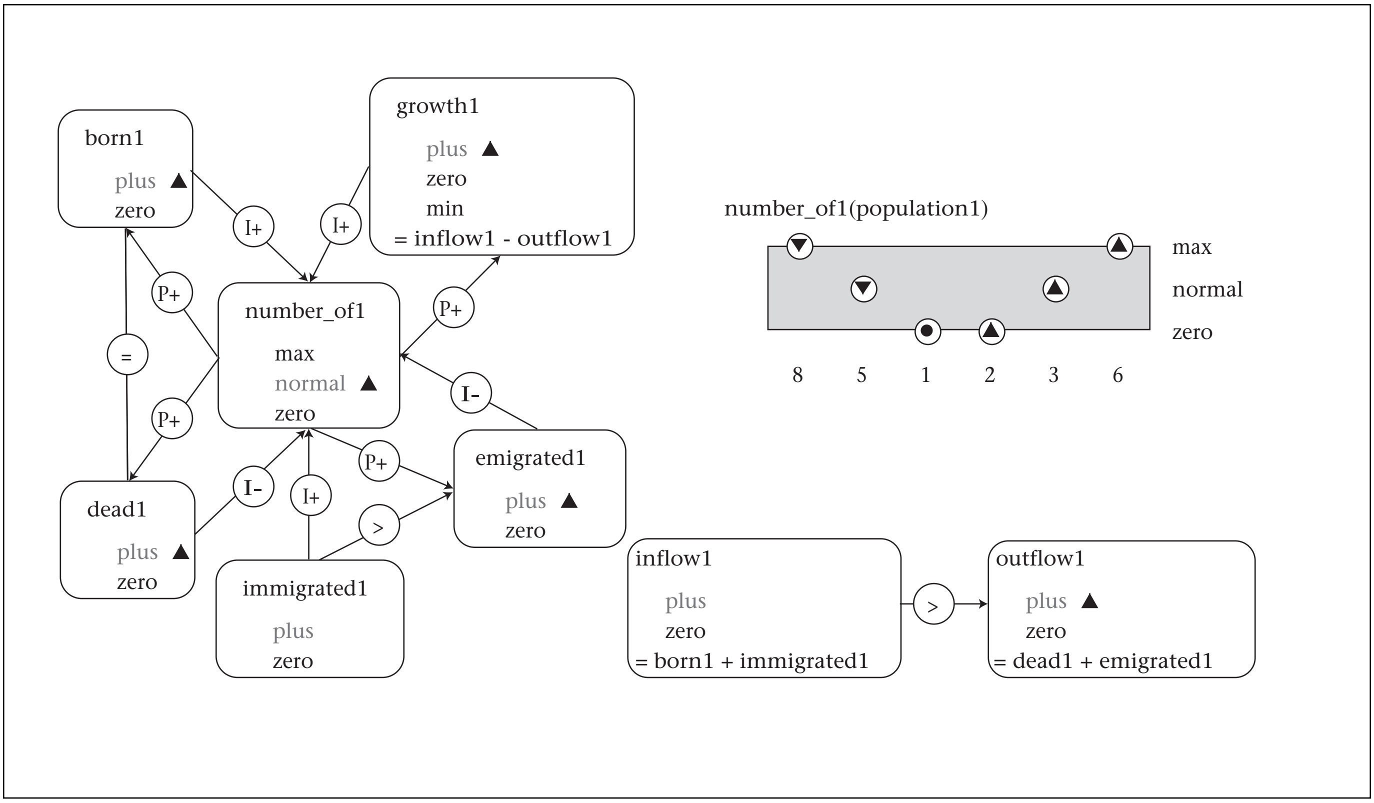

Figure 3. Simulation of a Population's Behavior, with Undefined Initial Values.

ulation is designated—when it changes in the opposite direction compared to changes in the other population. That is, it decreases as the other population increases, or it increases as the other population decreases. Second, a population is designated 0 when it is not influenced. Third, a population is designated + when it changes in the same direction as the other population changes. For example, if the interaction between populations (*A, B*) is classified as (+, –), then population *B* (given the – sign) decreases when *A* increases, and *A* (given the + sign) decreases when population *B* decreases.

In practice, it can be difficult to establish whether a population has a negative (or a positive) influence on another population. Sometimes the effects of an influence change with time or under different circumstances. It also can happen that what seems to be negative for a population has, in fact, a positive effect, which is especially the case with evolutionary aspects (for example, a prey population can decrease in number but by means of natural selection, survivors develop better adaptive features). We address the problem of interactions between populations as it is traditionally addressed in textbooks.

Base Model for Interacting Populations

Suppose there is no interaction at all between two populations (*neutralism*). In this case, a simulation would generate a state graph showing the cross-product of all the possible behaviors of each population, as if they were alone. However, if the two populations interact, either in a positive or a negative way, this full set of behaviors will be reduced. In other words, modeling an interaction between two populations means adding extra knowledge in the form of constraints, causal dependencies, and so on, that capture behavior-limiting mechanisms as defined by ecologists for each interaction type. Based on Odum (1985), we have implemented interaction models of neutralism (0, 0), amensalism (0, –), comensalism (0, +), predation (+ , –), symbiosis (+, +), and competition (–, –) (Salles et al. 2002).

We assume that any interaction between two populations is established using the basic population processes. To simplify the simulations, we also assume that both populations are closed populations (only natality and mortality processes are active), bringing us to a general organization of all interaction types, the base model shown in figure 4.[4]

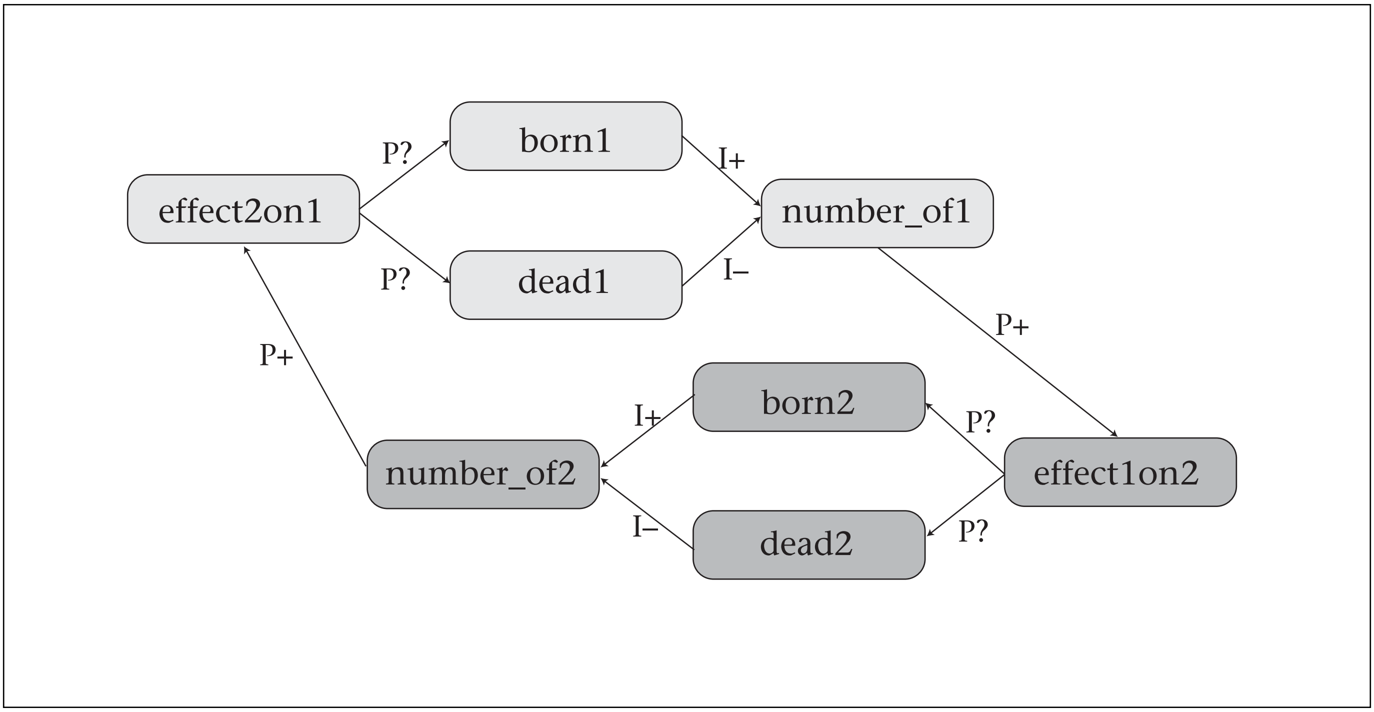

Figure 4. Base Model for Interactions between Two Populations.

Influences from one population (1) on another population (2), and vice versa, are represented by means of two quantities—(1) *Effect*1*on*2 and (2) *Effect*2*on*1, respectively—which, in turn, affect the *B* or *D* rates of both populations. In the real world, these influences between populations can be expressed in different ways (for example, increasing shade, offering shelter, producing chemical agents). The strength of the influence can also increase or decrease according to different factors other than the size of the influencing population (for example, shelter can be more important when there are more enemies around). To capture these distinctions in the model, it is important to use the intermediate quantity *Effect.*

The interaction is modeled using a number of indirect influences (*P*+, *P*–). Thus, the magnitude of the *Effect* is proportional to the size of the population that causes it. In addition, changes in the *B* and *D* rates are proportional to the magnitude of the *Effect* that influences them. The actual influence from *Effect* on the *B* and *D* rates differs for each interaction type, hence, the *P*? symbols. It can be a positive or a negative interaction, and the *Effect* can either influence both *B* and *D,* only one of the two rates, or none of them. Notice the semantics of the dependencies. For example, a positive influence from population2 on population1 can be represented as {*P*–(*D*1, *Effect*2*on*1) and/or *P*+(*B*1, *Effect*2*on*1)}.

Defining Interaction Types

To capture the behavior-limiting mechanisms for each interaction type (following Odum [1985]), modeling has to focus on the following aspects:

First is defining the *Effect* quantities that represent the interaction. For example, in the case of predation, the "effect" of the predator on the prey can be called *consumption* and the effect the prey has on the predator *supply.*

Second is establishing causal links between the quantities *Nof, Effect, B,* and *D* for both populations. Does *Effect* influence both *B* and *D*? Are they positive or negative influences? Notice that it follows from the base model that the influence from *Nof* on *Effect* is always positive.

Third is defining assumptions that implement correspondences and possibly other constraints between the quantities *Nof, Effect, B,* and *D*. For example, a simplifying assumption that we used in all the interaction models is the full correspondence between the *Nof* and the effect it causes. That is, the effect takes the same values as the *Nof.*

Fourth is representing conditions for nonexisting populations. With interactions, the nonexistence of a population can have an influence on the behavior of the other population, requiring reasoning about something (a population) that does not exist in the real-world system. For example, in our predation model, we assume that a predator population

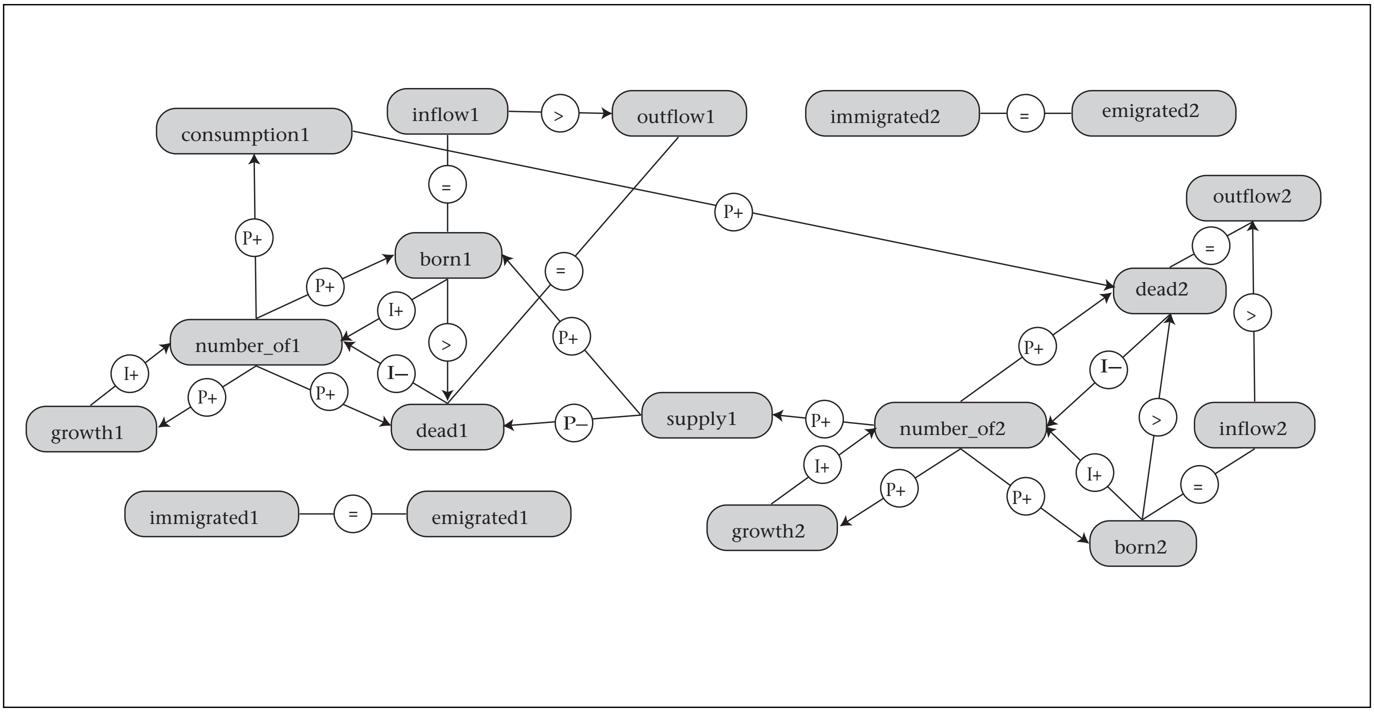

Figure 5. Causal Model for Predation.

cannot survive when the prey population goes extinct.

A separate set of model fragments capturing the points mentioned here is implemented for each interaction type. For details, see Salles et al. (2002).

Simulating Predation

A simulation with the predation model (+ ,–) can be used to illustrate some of the points. Figure 5 shows the causal model that holds in most of the states during the simulation.[5] States 5, 6, 7, and 8 have different causal models because in these states, at least one of the populations does not exist (see also discussion later). Notice that quantities with extension 1 refer to the predator, and those with extension 2 refer to the prey population.

For both populations, *Im* = *E* is true because of the closed-population assumption. It is assumed that *Supply* influences both natality and mortality of the predator, but *Consumption* influences only mortality of the prey. The state graph and the value history diagram shown in figure 6 are the result of a simulation starting with a scenario in which both populations have their normal size and an unknown direction of change; thus, *Nof* = <*normal,* ?>.

One of the assumptions included in this simulation is that the predator population cannot become bigger than the prey population, thus limiting the number of states generated by the simulator. Four interpretations are found for the initial scenario: states 1, 2, 3, and 4. Each of these states is the start of a subgraph representing one of four typical behaviors of a predator-prey system: (1) balanced coexistence, (2) populations to a maximum, (3) populations to extinction, and (4) predator to extinction.

Balanced coexistence: In state 2, the two populations have a natural balance; they coexist without further changes.

Populations to a maximum: State 1 leads to 10, optionally by 11, and shows the case in which both populations grow to their maximum size. Notice that the prey can reach its maximum size before the predator does (state 11) but not the other way around.

Populations to extinction: State 4 leads to 6, optionally by 5, and shows the case in which both populations disappear. The path using state 5 shows that the predator can become extinct before the prey but not the other way around.

Predator to extinction: Finally, state 3 leads to 8, optionally by 7 or 9. It shows that the predator no longer exists, but the prey population is still alive. Notice that the opposite is not possible.

By modifying assumptions (for example, allowing the predator population to become bigger than the prey population), different simulations are produced. In fact, the qualitative

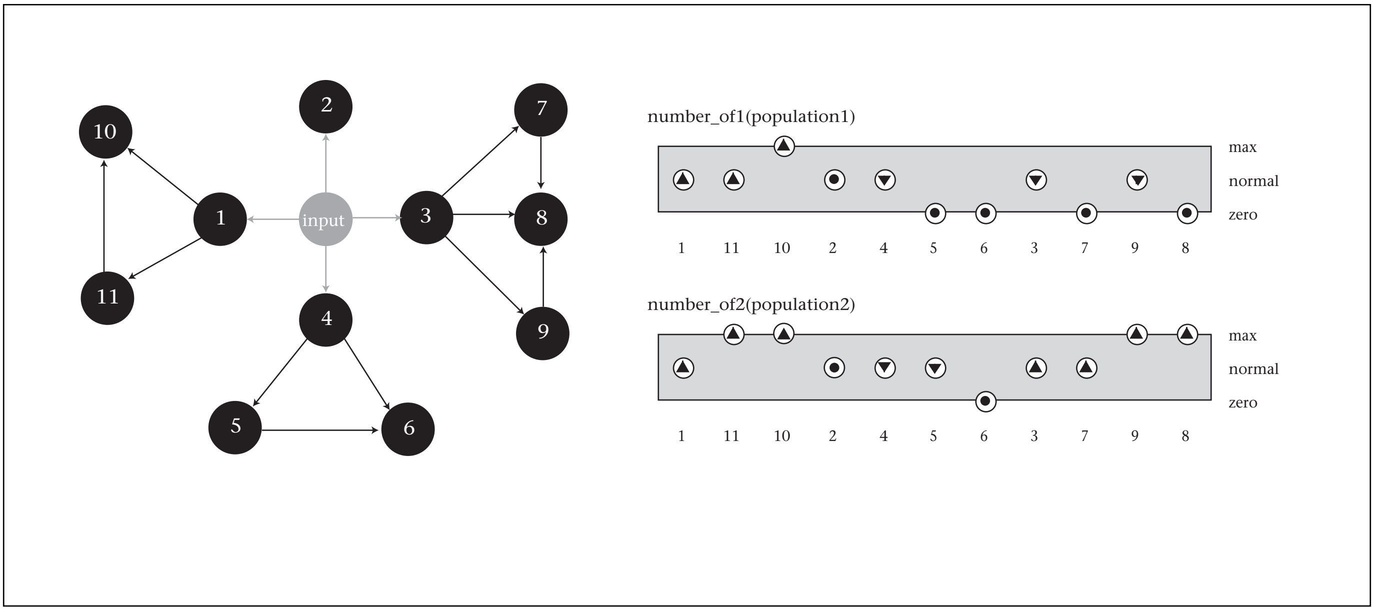

Figure 6. A Simulation with the Predation Model.

models presented here are rich in this respect, which makes them particularly interesting for studying and understanding different types of interaction. Understanding such interactions is important for establishing knowledge about the structure and behavior of communities, which, in turn, is important for answering theoretical and practical questions in educational and training situations.

Communities and Environmental Factors

This section presents the application of our qualitative domain theory about population dynamics for modeling complex community behavior, particularly the influence of environmental factors on terrestrial communities. Our models focus on succession in the Brazilian cerrado vegetation. This vegetation consists of many different physiognomies, spanning from open grasslands to rather closed forests. These communities have well- defined floristic composition mainly determined by fire, soil fertility, and water availability. According to a widely accepted commonsense hypothesis, changes in fire frequency can cause structural changes in the cerrado vegetation (for example, Coutinho [1990] and Moreira [1992]). If fire frequency increases beyond natural levels, woody components of Cerrado communities decrease, and graminoid components increase, so that the vegetation becomes less dense. If fire frequency decreases, the vegetation tends to become woody and denser. We refer to these increases and decreases as the *cerrado succession hypotheses* (CSH). Experts explain the succession behavior in terms of differences between tree and grass species. Germination and survival of young plants of tree species are more likely in shaded, cold, and moist microenvironments, but grass species do better in brighter, warmer, and dryer microenvironments.

A fully implemented qualitative model of CSH is presented in Salles and Bredeweg (1997). This model captures a conceptual explanation of the cerrado community behavior, as developed by experts. In this model, the vegetation is represented by functional groups of plants with similar behavior when exposed to certain environmental factors. With this approach, cerrado communities consist of three populations: tree (*T*), shrub (*S*), and grass (*G*). The qualitative domain theory about population dynamics discussed earlier can be applied to these populations.

Cerrado Community Types

Different proportions of grass, shrubs, and trees characterize the different types of cerrado communities. To capture this diversity in our model, the quantity *Nof* has been given a five-valued quantity space, *QS* = {zero, low, medium, high, max}. Model fragments are used to represent the community types (figure 7). The most important ones are campo limpo, campo sujo, campo cerrado, cerrado sensu stricto, and cerradão. This sequence presents a gradient in which campo limpo has no trees and no shrubs, only grass. At the opposite end, cer-

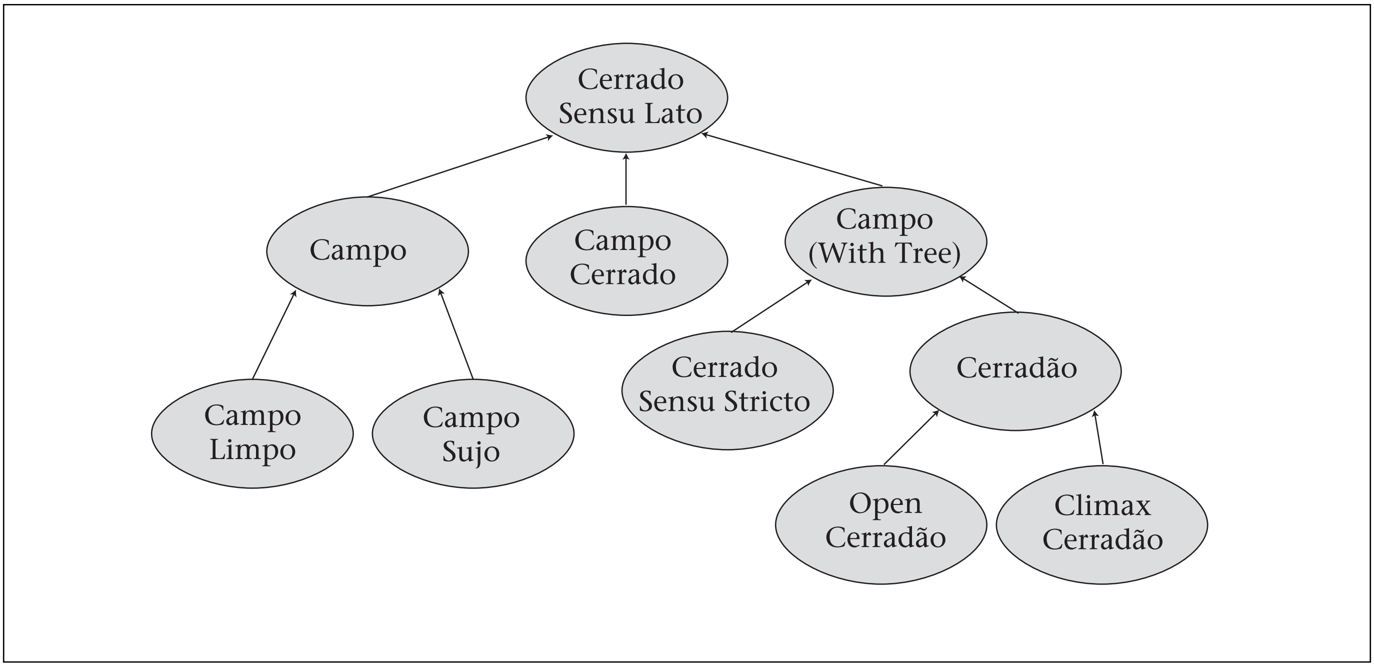

Figure 7. Overview of the Most Typical Cerrado Communities.

radão is the most dense forest, with no grass, only tree and shrub populations. In between these types, there are communities with increasing amounts of shrub and trees and less grass. The cerrado sensu lato model fragment represents environmental factors that apply to all community types.

Causal Model of the Cerrado Succession Hypotheses

The causal dependencies are shown in figure 8. In this figure, number_of1 (*Nof*1) refers to the tree population, number_of2 (*Nof*2) to shrubs, and number_of3 (*Nof*3) to grass. The most important quantities in the model are fire frequency, litter, moisture, light, soil temperature, and nutrient. These quantities are related to each other by proportionalities (*P*+, *P*–) and build a causal chain by means of which fire frequency affects litter, which, in turn, affects the four other quantities. An additional set of model fragments encodes knowledge about how these environmental factors affect the basic processes in the three populations. Tree and shrub populations are influenced differently by light and soil temperature compared to the grass population. For example, in tree and shrub populations, *light* has a positive influence on the mortality process, thus {*P*+(*D, Light*)}, but in the grass population, this influence is negative: {*P*–(*D, Light*)}. The influences, ultimately caused by the fire frequency, are further strengthened by a positive feedback loop involving *cover,* a quantity that represents the shade of trees; hence, {*P*+(*Cover*, *Nof1*)}.

Control over fire frequency is modeled as a human action, using the notion of an agent model (Bredeweg 1992). In this case, the agent model puts a direct negative influence on the quantity *fire frequency* by means of a quantity (rate) called *control*, thus {*I*–(*Fire-frequency, Control*)}. Quantity control rate has a tree-valued quantity space: *QS* = {min, zero, plus}, representing a negative, an ineffective, and a positive control, respectively. Two versions of this agent model are implemented in the model: (1) *decrease fire frequency* (a positive control so that Control = <plus, 0>) and (2) *increase fire frequency* (a negative control so that Control = <min, 0>). The effect is assumed to be constant during a simulation.

Simulating the Cerrado Succession Hypothesis

Simulations with this model show, as expected, the transitions between the community types caused by control measures on fire frequency. For example, it is possible to simulate that when the fire frequency is decreased, a community of campo limpo can change to campo sujo because the grass population (*Nof3*) decreases, but shrub (*Nof2*) and tree (*Nof1*) populations increase. If the conditions stay the same, campo sujo becomes denser and changes toward different communities until the most dense community is reached (climax cerradão). Figure 9 shows this behavior graph and the value history diagram for the three populations.

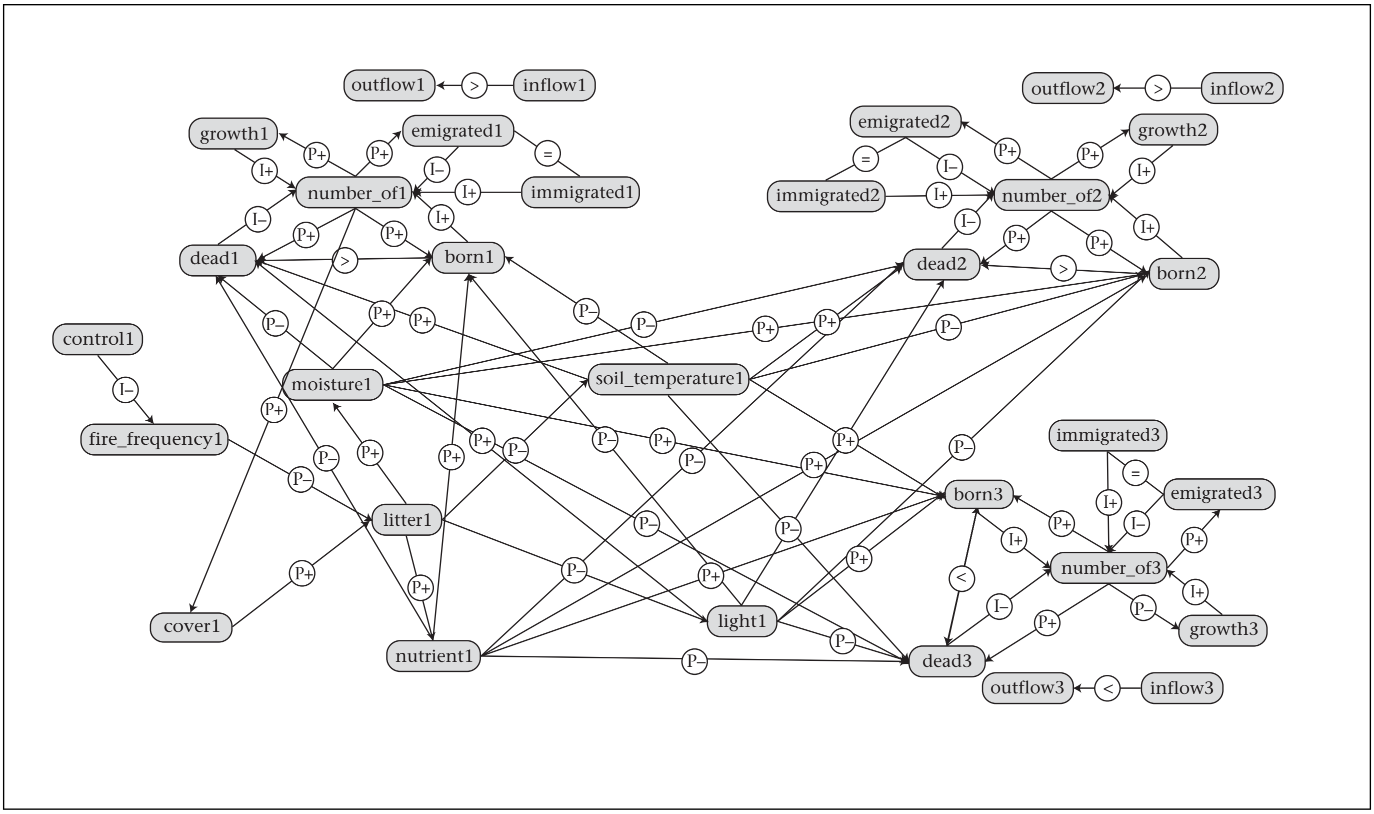

Figure 8. Causal Dependencies for the Cerrado Succession Hypothesis.

Succession can be illustrated following the behavior path: campo limpo (states 1 and 4), campo sujo (state 5), campo cerrado (state 12), cerrado sensu stricto (state 13), open cerradão (state 15), and climax cerradão (state 16). The grass population tries to enter again using colonization (transition from 16 to 18). However, this colonization does not lead to new states (there are no successors of state 18) because the grass population cannot grow unless shrub and tree populations decrease. Notice that by setting different initial values, we can also simulate alternative behaviors. For example, imposing a negative control (increasing fire frequency) on a climax cerradão community produces a simulation showing the degradation behavior in which the closed forest is reduced to open grassland (campo limpo).

Status and Implementation

The CSH model is a large qualitative model. Consider, for example, state 12, the campo cerrado community. This state is described by means of 61 model fragments, including 19 active processes. These model fragments introduce 20 objects, which are associated with 32 quantities constrained by 127 different relations. The current implementation of the models described in this article includes nearly a hundred initial scenarios. By changing the initial values of quantities (magnitudes and derivatives) and modeling assumptions, this number can easily be augmented without introducing any further knowledge to the library. The resulting simulations are conceptual models that capture considerable amounts of ecological knowledge as articulated by domain experts.

Related Work

Representing qualitative knowledge has long been an outstanding problem in ecological modeling. Pivello and Coutinho describe a preliminary prototype that models the succession phenomenon in the cerrado.[6] They use a typical rule-based approach in which rules specify the conditions for state transitions between the different types of cerrado vegetation. They identified 11 types of communities and 42 possible transitions, corresponding to fire, grazing, and woodcutting under different environmental conditions. The resulting model is qualitative, in the sense that it does not use any numeric data, and simple enough to be understood and used by managers of cerrado conservation areas. However, as is typical for rule-based systems, the knowledge represented

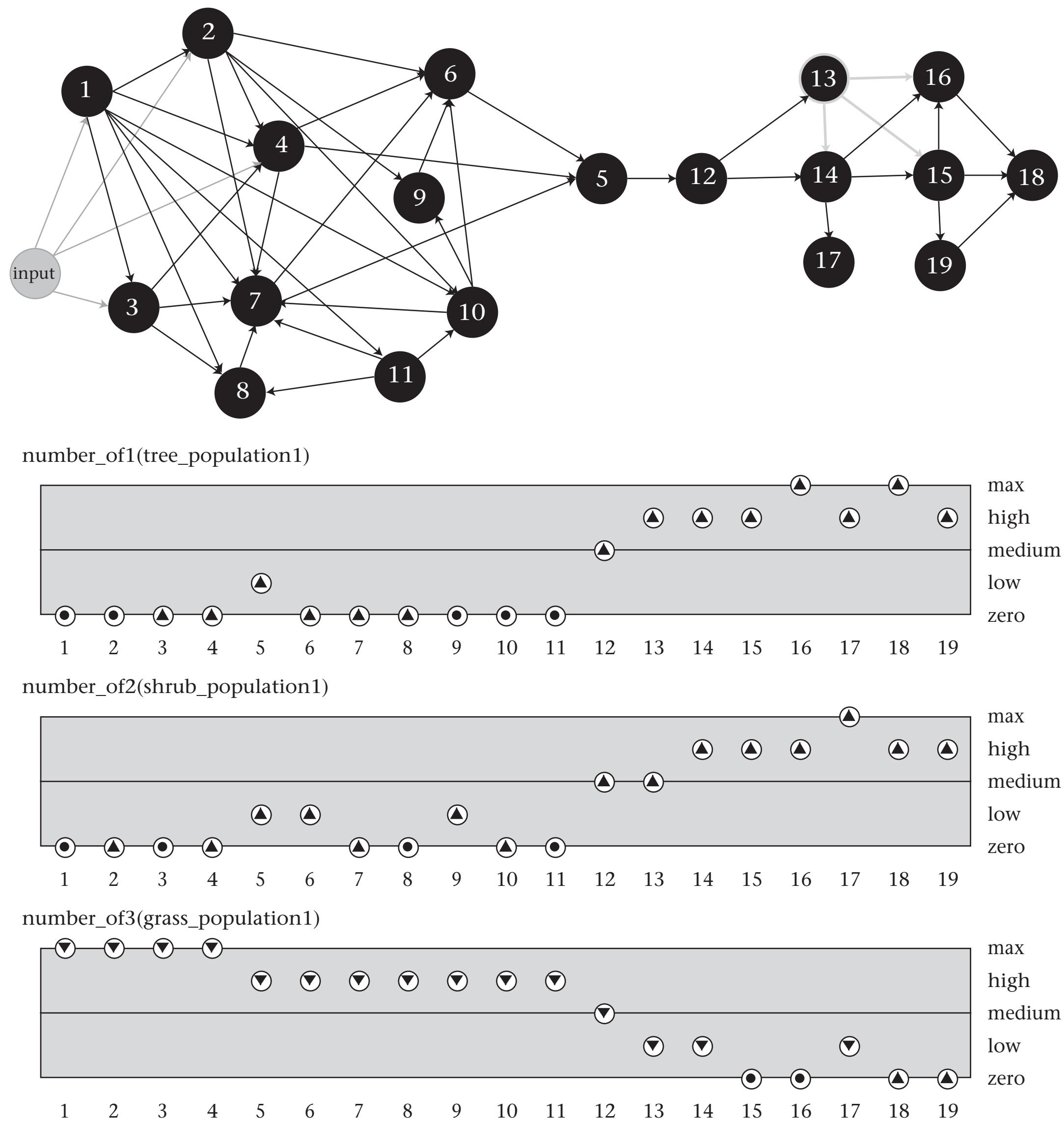

Figure 9. Simulation with the Cerrado Succession Hypothesis.

in the rule base is shallow and does not implement the underlying principles that actually explain the working of the succession phenomenon.

Noble and Slatyer (1980) address qualitative aspects when they discuss community dynamics subject to recurrent disturbance (such as fire), based on a small number of attributes of the plant's life history (vital attributes). Their simulations typically produce a replacement sequence that depicts the major shifts in composition and dominance of species following a disturbance. Moore and Noble (1993, 1990) combined this approach with knowledge about the abundance of the populations and their survival to describe which of the several species, at a comparable life stage, might be dominant in terms of bio-mass or density. However, these aspects are handled using mathematical models, and only the final output is presented in qualitative terms such as {low, medium, high}.

Only a few researchers have tried using a full qualitative approach. Guerrin and Dumas (2001a, 2001b) discuss models representing the functioning of salmon spawning areas and the impact this phenomenon has on mortality in early stages. They successfully used QSIM (Kuipers 1986) to generate qualitative predictions on the survival rate of salmon under various scenarios. Kamps and Péli (1995) present a population-oriented approach to model economical phenomena. They constructed a qualitative version of the logistic equation, using GARP (Bredeweg 1992), to model the dynamics (natality and mortality) of companies. May (1973) describes a model that uses only the signs {–,0, +} to represent the dynamics of populations connected in a food web using interactions such as predation, competition, amensalism, comensalism, and symbiosis. He shows that commonsense wisdom might not be true: A less complex community met the conditions for stability, but the more complex was not stable.

Conclusion and Discussion

This article describes long-term research on the development of qualitative models and simulations about ecological systems involving population and community dynamics. To capture and simulate commonsense ecological theories, as articulated by experts, we have developed and implemented a qualitative theory of population dynamics. This theory is used as the basis for simulating models of typical interaction types between two populations. It is also used to express how environmental factors influence the behavior and composition of vegetation communities. Specifically, we show how predictions for the Brazilian cerrado community, following from the CSH, can be generated using partial models of the basic processes that govern the behavior of the individual populations.

Combining partial models to scale up to more complex models is a desirable feature in ecological modeling. A compositional approach enabling reusability of previously defined parts provides the modeler with the possibility to gradually increase the complexity of the models. Moreover, it facilitates the representation of fundamental knowledge that can be used to simulate and explain more complex phenomena.

The models presented here are conceptual models and do not require any numeric data. The qualitative representation provides a rich vocabulary for describing objects, situations, causality, and mechanisms of change. This vocabulary can be used to express knowledge that is, in general, difficult to represent using a mathematical approach. The results produced by simulating these models show that conclusions relevant to ecologists can be derived automatically using only qualitative knowledge. This important characteristic demonstrates the potential of qualitative models as a valuable complement for mathematical approaches to ecological modeling.

Future work on qualitative ecological modeling has many interesting possibilities. One of our themes focuses on further developing and applying our approach to represent the behavior of other large communities. Ongoing work also includes the development of tools to support educational and management activities based on articulate simulations, notably on terrestrial ecology and water resources management. Particularly, we have developed guidelines for constructing learning routes through complex qualitative simulations to support learners in understanding and acquiring the knowledge captured in such models (Salles and Bredeweg 2001). In Salles, Bredeweg, and Winkels (1997), the authors describe how explanations can be generated, as part of an interactive dialogue, using the didactic principles and discourse strategies developed by Winkels (1992). We believe that it is important to work simultaneously on both knowledge capturing and knowledge sharing because knowledge sharing determines the degree of articulateness required in knowledge capturing. After all, an important consequence of knowledge articulation is the common desire of wanting to share the newly created insights with others.

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This article is dedicated to Eugene Odum, who opened up new ways of thinking about ecology.

Notes

1. Software and models can be downloaded from www.swi.psy.uva.nl/projects/GARP/.

2. Behaviors resulting from ambiguity should not be confused with spurious behaviors (for example, Kuipers [1986]). *Spurious behaviors* refer to incorrectly predicted behaviors that do not occur for the real system. *Ambiguity* refers to alternative correct behaviors predicted because information is lacking.

3. All simulation results are shown using VISIGARP (Bouwer and Bredeweg 2001). VISIGARP implements a graphic user interface on top of GARP.

4. All quantities with extension 1 belong to population 1 and with extension 2 to population 2.

5. Notice that figures 3 and 5 originate from the same VISIGARP view on the simulation, although less information is shown in figure 5.

6. Pivello, V. R., and Coutinho, L. M. 1995. A Successional Model to Assist on the Management of Brazilian Cerrados. Unpublished manuscript. Department of General Ecology, University of São Paulo, Brazil.

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