Qualitative Models of Interactions between Two Populations

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Abstract

This paper presents qualitative models of interactions between two populations in biological communities. Negative and positive interactions like competition, predation and symbiosis are considered determinant factors in the structure of communities and are important topics in ecological theory and practice. Qualitative simulations can be used for representing such ecological knowledge in interactive learning environments. Using the qualitative theory about population dynamics already implemented in GARP, we created qualitative simulation models to support predictions about some of the most common behaviours of two interacting populations. Modelling assumptions are explicitly represented and therefore can be analysed by students and modellers. We briefly discuss how these models can be organised to create interesting learning routes.

Introduction

This paper presents qualitative simulations of interactions between two populations in biological communities. Qualitative simulations are detailed and articulate knowledge models representing insights humans have developed of systems and their behaviour. Such knowledge models are interesting, both from an ecological and an educational perspective.

Historically, in the field of ecology, models about two populations are based on matrices and the logistic equation (*cf.* Haefner, 1996; Jørgensen & Bendoricchio, 2001). Qualitative models provide new opportunities for articulating ecological knowledge. Particularly, to represent those aspects which are normally hard to capture in quantitative models, such as explicating causal insights and dealing with incomplete, sparse and qualitative knowledge.

From an educational point of view, qualitative simulations can (similar to quantitative simulations) be used as the basis for learning environments, exploiting the added value of using simulations for education purposes. In addition, qualitative models provide a rich vocabulary for learners to interact with and engage in knowledge construction activities. The latter even more now that graphical tools have been developed that support learners in inspecting qualitative simulations (*cf.* Bouwer & Bredeweg, 2001).

Ecological theories usually take the position that biological communities are organised according to positive and negative effects coming from interactions with other organisms, in the context of physical (environmental) factors (*cf.* Odum, 1985; Krebs, 1994). Examples of such interactions are 'competition', 'predation', 'parasitism', and others. However, qualitative simulations of such interactions currently do not exist.

Our previous work describes the development of a qualitative theory of population dynamics (Salles & Bredeweg, 1997). Using this library of basic processes it is possible to derive complex community behaviour from 'first principles' in ecology. For example, we have implemented the 'Cerrado Succession Hypothesis', a set of simulation models about the succession process in the Brazilian Cerrado vegetation (see Salles & Bredeweg, 2001).

In this paper we further refine the idea of explaining community behaviour from first principles by explicating how the interactions between populations affect the basic processes for individual populations (and as a consequence affect the overall behaviour of the community). We describe an implemented set of qualitative models about the interactions between two populations of different species and discuss how to use them in educational contexts. The resulting simulations show the typical behaviours of pairs of interacting populations.

Ecology of interactions between two populations

Communities are defined as set of populations of different species living in the same space during the same period of time. Most ecologists believe these species are not randomly associated, and how communities are structured has been subject of an intense debate. Negative and positive interactions between populations such as competition, predation and symbiosis, working under the influence of physical factors of the environment, have been pointed out as the main organising forces of communities. The roles of competition and predation in organising communities have been emphasised by many authors (*cf.* Odum, 1985; Krebs, 1994).

Relationships between 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. When these details are left out and just the effects are considered, interactions can be classified according to combinations of the symbols {−,0,+} as follows: (a) 'minus' means that one population is adversely affected by the other; (b) 'zero' means that one species suffers no effects from the other population; and (c) 'plus' means that one population receives benefit from the other species. If the interaction is to be modelled as an equation, the meaning of the symbols is to add a positive or a negative term to the growth equation of both populations. Mechanisms and effects of main interactions between two populations, as described by Odum (1985), are summarised below (format: Interaction type species(1,2): Comments)

- Neutralism (0,0): None of the populations affects the other population.
- Amensalism (0,–): Population1 inhibits population2, in general by producing some toxic substance (and population1 is not affected).
- Commensalism (0,+): Population1 benefits population2, in general providing food or transport (and population2 is not affected).
- Predation (+,-):Population1, the predator, causes harm to population2, the prey, and is benefited by the interaction; often the predator is bigger than the prey and less numerous.
- Parasitism (+,-):Population1, the parasite, causes harm to population2, the host, and is benefited by the interaction; often the parasite is smaller than the host and more numerous.
- Herbivory (+,-): Population1, the herbivore, causes harm to population2, the plant, and is benefited by the interaction; this involves eating fruits, seeds, leaves and other parts of the plant.

- Protocooperation[*] (+,+): Both populations benefit, but it is a non-obligatory interaction.
- Mutualism[*] (+,+):Both populations benefit, it is an obligatory interaction (for one or both populations).
- Competition by interference (-,-): Each population is directly inhibited by the other population.
- Competition by resource exploitation (-,-): Both species have the same requirement and the common resource is in shortage (indirect inhibition).

Models representing interactions between populations are useful for the development of strategies of conservancy in natural ecosystems, or in programmes of recuperation of degraded land. For example, according to Morosini & Klink (1997), 'molassa grass' (*Melinis minutiflora*) is one of the most aggressive invading species in the Brazilian Cerrado vegetation. This African species can cause disruptions in the invaded area, and is benefited by fire. It has been shown that after burning, *Melinis* occupies the space leaving out native species. However, shaded by trees like *Cecropia* the grass can be eliminated. This interaction can be seen as (–,–).

Positive interactions such as commensalism and symbiosis are also reported in the literature about the Cerrado. Mendonça & Piratelli (1997) feed animals from eight vertebrate species on fruits and made germination tests with the seeds. They found some good potential dispersors of seeds, like monkeys from genus *Cebus*. Nearly all of the studied species had increased seed germination after passing through the animal digestive system. It can be seen as protocooperation, with positive effects for the plants (dispersion and germination) and for the animals that feed on them.

Interactions between two populations may change under different conditions or in different stages of the life cycle. This is for instance the situation involving insects of two orders (Hymenoptera and Lepidoptera), described by Scherrer *et al.* (1997) in the Cerrado. Hymenoptera are *parasitoid* insects, *i.e.* larvae of Hymenoptera kill carterpillars (larvae of Lepidoptera) but do not affect adult Lepidoptera. This way, interaction between these insects can be described as follows: (a) larvae of Hymenoptera and larvae of Lepidoptera, (+,–); (b) larvae of Hymenoptera with larvae or adults of Lepidoptera, (0,0); (c) adults of both, (0,0).

In summary, communities are complex webs of relationships and the interactions between pairs of populations can change over ecological and evolutionary time scales.

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[*] Protocooperation and mutualism are called also *symbiosis*.

Qualitative models of interactions between populations

Salles and Bredeweg (1997) present the development of a qualitative theory of population dynamics. This theory is implemented using the domain independent qualitative reasoning engine GARP (Bredeweg, 1992) and can be employed to run simulations involving basic processes. Figure 1 shows some of the results produced by the simulator[1].
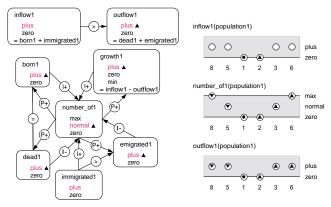

Figure 1: Basic processes influencing a population

The value history diagram (right part of the figure) shows that a behaviour path starts with a maximum sized population (state 8). Next, the population becomes zero (extinct) (state 1) and after colonisation (state 2) becomes full sized again (state 6). The size of a population is represented by the quantity '*number_of* individuals' (*Nof*). In the simulator each quantity has a quantity space (QS) specifying the values that it can take on. For the simulation shown in figure 1 *Nof* can take on three values, QS={*zero, normal, max*}. Furthermore, in each state of behaviour all quantities are represented as magnitude/derivative pairs, V=<*mag, der*>. For instance in state 8, *Nof* is represented as <*max, min*>. The causal model underlying each state can be inspected and figure 1 shows the details for state 3 (left part of the figure). In this state the four basic processes are active (*natality*, *mortality*, *immigration* and *emigration*). Each of these processes influences the size of the population (*e.g., mortality* has a negative influence, *I-*). At the same time changes in the population affect the basic processes (*e.g.,* when the size of the population increases, *mortality* will also increase, *P+*). The figure also shows how the different flows can be accumulated into the total *inflow* and *outflow* and how these flows eventually

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[1] Limited space in this paper does not allow for presenting all the knowledge that is derived by the simulator. For instance, each state has a set of model fragments that have been found to be applicable and from which the causal model is constructed. Model fragments (and their contents) are important enablers of knowledge communication in an educational context. Also, each state-transition captures detail with respect to what is changing between the two states. For further details see (Bredeweg, 1992).

determine the overall population *growth*.

The simulation discussed here is only one of many alternative simulations that can be run. Such simulations typically vary on assumptions, initial values, and initial inequality statements between the quantities involved. In a learning situation, students (working individually or in pairs) are given assignments that they have to solve by inspecting simulations. E.g., explaining why colonisation does not happen in the case of a 'closed' population[2].

Using the library of model fragments, which implements a qualitative theory of population dynamics, it is possible to derive complex community behaviour from 'first principles' in ecology. We have, for example, implemented the 'Cerrado Succession Hypothesis', a set of simulation models about the succession process in the Brazilian Cerrado vegetation (see Salles & Bredeweg, 2001). Below we further detail the interactions between two populations using the same model fragment library as a basis.

Base model of interactions between 2 populations

Suppose there are two populations that do not interact. If there are no constraints, all the possible behaviours (that each population alone can exhibit) are expected to appear in a simulation. Therefore, all the combinations of values (magnitudes and derivatives) of all quantities for the two populations will be found. However, when the populations are not independent, but interact and affect each other, we expect that some of these behaviours will be restricted. That is, not all behaviours can be expressed by both populations. Modelling these interactions means articulating the *constraints* that limit the set of possible behaviours for the two populations.

As a starting point we define a 'basic interaction model' for capturing interactions between two populations. The simplest version of that model in shown in figure 2. Population1 produces some effect (*effect1on2*), which in turn affects natality (*born2*) and mortality (*dead2*) of population2. In the same way, population2 produces an effect on population1 (*effect2on1*) which influences natality (*born1*) and mortality (*dead1*) of population1. These influences are modelled using qualitative proportionalities, represented in figure 2 as {P+, P–, P?}. Notice, the difference between *P* and *I*. Influences (*I*) represent flows. Proportionalities (*P*) propagate changes.

An important aspect of modelling is the use of assumptions. In our approach assumptions are explicitly represented as model fragments in the library[3]. A first assumption to be made is that we are focussing on non-migrating populations (the 'closed-population' assumption).

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[2] 'Closed-population' is an assumption ecologists use to focus on situations in which no individuals enter or leave the population.
[3] A distinction is made between operating and simplifying assumptions. However, in this paper we will not discuss this distinction and refer to both as 'assumptions'.

That is, the quantities *emigration* (*E*) and *immigration* (*I*) are part of all models (because they are part of the basic processes), but it is assumed that their influence on the interactions is zero: $E=<0,0>$ & $I=<0,0>$. Consequently, input for the qualitative growth equation comes only from *natality* (*B*) (*inflow = B*), output from *mortality* (*D*) (*outflow = D*), and the equation becomes *growth = B – D*.
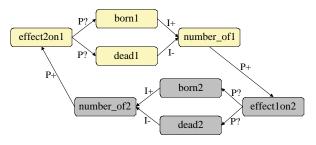

Figure 2: Base model for representing interactions between two populations

The next step is to refine the basic interactions (as shown in figure 2) for each type of interaction (as shown in table 1). The result is shown in table 1. The idea is that the populations are influenced *via* their basic processes. A negative influence decreases natality and/or increases mortality. Similarly, a positive influence increases natality and/or decreases mortality.

Interaction	Influences	Models
Competition (-,-)	Effect1on2 is negative Effect2on1 is negative	P-(Born2, Effect1on2) P+(Dead2, Effect1on2) P-(Born1, Effect2on1) P+(Dead1, Effect2on1)
Amensalism (0,-)	Effect1on2 is negative Effect2on1 none	P-(Born2, Effect1on2) P+(Dead2, Effect1on2)
Neutralism (0,0)	Effect1on2 none Effect2on1 none	no relations between the two populations
PredatorPrey (+, -)	Effect1on2 is negative Effect2on1 is positive	P-(Born2, Effect1on2) P+(Dead2, Effect1on2) P+(Born1, Effect2on1) P-(Dead1, Effect2on1)
Commensalism (0,+)	Effect1on2 is positive Effect2on1 none	P+(Born2, Effect1on2) P-(Dead2, Effect1on2)
Symbiosis (+, +)	Effect1on2 is positive Effect2on1 is positive	P+(Born2, Effect1on2) P-(Dead2, Effect1on2) P+(Born1, Effect2on1) P-(Dead1, Effect2on1)

Table 1. Main interaction types according to the effects on population growth.

In summary, population attributes are represented by the quantities {*Nof*, *B*, *D*, *I*, *E, growth* and '*effect*'}. Quantity spaces associated to these quantities: *Nof* has QS = {zero, normal, maximum}; *B*, *D*, *I* and *E* have QS = {zero, plus}; derivatives of all quantities and *growth* have QS = {–,0,+}; *effect1on2* and *effect2on1* have the same QS as *Nof*.

Having set up the basic architecture, each interaction type

can be constructed following a set of modelling steps. First, determining the specific quantities that implement the *'effect'* for each interaction. Second, establishing the causal links between quantities *Nof*, *B*, *D* and '*effect*' (e.g. sometimes only *B* is affected and not *D*). (Notice that both activities are further refinements of table 2). Third, assumptions have to be specified that capture correspondences between quantities. For instance, are *consumption* and the *Nof* prey, in the case of a predator-prey interaction, 'full corresponding' quantities? If so, this has to be included in the model. Fourth, there are assumptions that can be made to simplify the simulations results. Usually they are independent of the interaction effect and reduce the ambiguity. An example could be to keep the derivatives of *B* and *D* equal, so they undergo similar changes if both are equally influenced by the quantity *'effect'*.

We have found that some assumptions make sense in most interaction types. One such assumption concerns the relation between *Nof*, *B* and *D* in one population. In principle, all kinds of variation are possible (*e.g.*, *Nof*=<plus,plus>, *B*=<plus,min>, *D*=<plus,plus>, or *Nof*=<plus,plus>, *B*=<plus,plus>, *D*=<plus,min>, etc.), but it is usually of little importance to the typical behaviour of an interaction type. To simplify the matter, it is assumed that (1) *B* and *D* are full corresponding, and (2) that *D* and *Nof* always change in the same direction (in some interaction types *B* is also included). Another assumption concerns *Nof* in relation to the *'effect'* quantity (caused by *Nof*). In some interaction types they are assumed to be full corresponding, whereas in other types it is assumed that *Nof* is always greater or equal to *'effect'*, but the *'effect'* can never exceed the *Nof*.

Finally, the base model of two population interactions includes views of qualitative states in which one of the populations does not exist. This is relevant because in some interactions it may happen that one population cannot exist if the other does not exist. Problems and modelling solutions specific to each particular interaction model are discussed next.

Predator-prey model (+,-)

The behaviour we want to represent with this model shows the predator population changing along with the prey population. To achieve that, the model uses the base model shown in figure 2 except in one aspect: negative influence of the predator (population1) affects only *mortality* of the prey (population2). Figure 3 shows the dependencies as they actually appear in the simulation (without derivative constraints).

The general constraints, as discussed above, imply that the consumption of food (*effect1on2*) is equal to the predator population size (*Nof1*) and supply of food (*effect2on1*) is equal to prey population size (*Nof2*). In fact, *consumption* depends on many factors, such as the ability of predator to

catch the prey and the availability of alternative sources of food. *Supply* depends on the ability of prey to avoid the predator and the existence of refuges in the environment. Thus, our assumptions implement an approximation of the full natural phenomena.
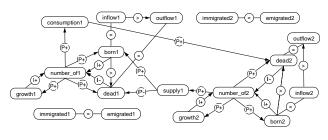

Figure 3: Causal dependencies in predator-prey model

Specific restrictions are that the predator population cannot become bigger than the prey population nor survive without it. This is modelled by stating that when *Nof1* is zero, so is *Nof2*. Complementary to that, it is assumed that the *supply* (*effect2on1*) has to be equal or greater than *consumption* (*effect1on2*), and that the latter cannot increase faster than the former.

A simulation with this model is presented in figure 4. Starting with an initial scenario in which both populations have *Nof* =<normal,?>, four initial states are found. The full simulation produces 11 states showing all the possible behaviour paths possible under the set of constraints: coexistence with normal sized populations (state 2), both populations at their maximum size (state10), predator extinct and prey at maximum (state 8) and both populations extinct (state 6).
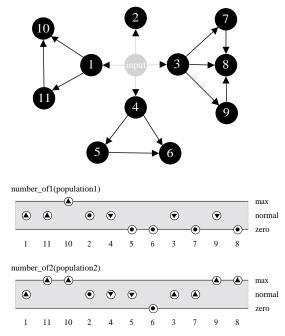

Figure 4: Behaviour states for a scenario within the predator-prey model

Competition by interference (-,-)

This model should express coexistence and competitive exclusion of one population. Compared to the predator-prey model, there is a difference: the derivatives of *B2* and *D2* are assumed to be equal, as it happens with the derivatives of *B1* and *D1*. This way, *B2* and *D2* show the same behaviour, which is, in turn, determined by *effect1on2*.

Effect1on2 can be greater, equal or smaller than *effect2on1*. These conditions are expressed in three different initial scenarios. It is assumed that the derivatives of both '*effect*' quantities follow the same inequality relation expressed by the magnitude. For example, if *effect1on2* is greater than *effect2on1*, its derivative is also greater. With these assumptions, *effect2on1* will not become bigger than *effect1on2* during the simulation.

Simulations with this model show competitive exclusion of population1, population2 and coexistence, depending on the relative magnitudes and derivatives of *effect1on2* and *effect2on1*. If *effect1on2 = effect2on1*, negative influences have the same strength in both populations and competitive exclusion does not occur. From the initial scenario with both *Nof*=<normal,?>, three states are produced with the derivatives of *Nof1* and *Nof2* having the same value. The full simulation produces seven states in which both populations are stable at their normal size, both go to maximum or both go to zero.

If the interaction is asymmetric, competitive exclusion occurs and the competitor with greater '*effect*' on the other population wins. Starting with the same initial scenario, three initial states arise. In two of them, both *Nof* have equal derivatives (increasing or decreasing). Stability for both is not possible. In the third initial state, the different strength of the negative effects results in the strongest population increasing and the weakest decreasing. In the example, the third initial state has *Nof1*=<normal,-> and *Nof2*=<normal, +>. This will lead to the competitive exclusion of the weakest. The behaviour graph is the same for both situations, with 10 states in the full simulation.

An extension of the model above could include such influences on the interaction. For example, suppose fire frequency decreases due to management practices. Under this condition, it may happen that *effect1on2 > effect2on1* and population2 is excluded. Alternatively, if fire frequency increases, *effect1on2* may become smaller, changing the results of competitive exclusion. This can be used to predict the behaviour of the interaction between *Melinis* and *Cecropia* (Morosini & Klink, 1997), already mentioned.

Commensalism (0,+)

This model has to represent one population increasing

when the other increases, without influencing the latter. In addition, we also want to represent: (a) situations in which the size of population2 (the one that receives the *benefit*) is limited by the size of population1 (the one that produces the *benefit*), and (b) situations that express the effects of *benefit* with different magnitudes.

The base model (figure 2) and the associated set of constraints are enlarged with more details in order to produce behaviour that satisfies these requirements. Assumptions about the derivatives of *B* and *D* are the same for both populations and similar to the competition model. It is assumed that the *benefit* produced by population1 is essential for the survival of population2. This way, if *Nof1* is zero, *Nof2* goes to zero as well.

In order to limit combinations of possible population sizes, explicit associations involving the magnitudes of *benefit* and *Nof2* are introduced in the model. For instance, *Nof2* can only have value 'max' when *benefit* is also 'max'. If *benefit* has value 'normal', population2 cannot reach its maximum size.

To explore the strength of the effect of *benefit* on *Nof2* we used relations involving the derivatives. For instance, 'high impact' means that changes in population2 are fully determined by the *benefit*. This is achieved by stating that the derivative of *benefit* is equal to the derivative of *Nof2*. 'Medium impact' means that the *benefit* is partially responsible for changes in population2. This is modelled by assuming that the derivative of *benefit* is greater or equal to the derivative of *Nof2*.

Comparing simulations, it is possible to see how these assumptions influence behaviour. A simulation under the 'medium impact' assumption starting with the same initial scenario (both *Nof*=<normal,?>) produces five initial states, representing combinations of the derivatives of *Nof* in both populations. However, in none of them the derivative of *Nof2* is greater than the derivative of *Nof1* (remember that the derivative of *benefit* is determined by *Nof1*). The full simulation produces 13 states showing, at the end, (a) both populations stable at normal size; (b) both populations extinct; (c) population1 normal, stable and population2 extinct; (d) population1 max and population2 extinct; (e) both populations at full size (max). Assumptions about *benefit* and *Nof2* magnitudes reduce the number of possible states in the full simulation to 10. In none of them the magnitude of *Nof2* is greater than the magnitude of *Nof1* (remember that the magnitude of *benefit* is the same of *Nof1*).

Other models

The neutralism (0,0) model shows the non-interaction, a situation in which there are no influences between the two populations. Starting with an initial scenario in which both populations have *Nof* = <normal,?> the full simulation produces 25 states, showing all the combinations between

the values of magnitude and derivative of *Nof*. Given that all the other interactions are modelled by adding constraints on *natality* and *mortality*, this model can be seen as the 'base simulation model' for interactions between two populations.

The amensalism (0, -) model introduces different impacts of the negative effects depending on the size of population1 (the one that produces *pollution*). Simulations show that both populations can survive alone, and that population2 cannot become bigger than population1.

The symbiosis (+,+) model represents protocooperation (non-obligatory interaction) and assumes that the positive effects on both populations are equal. Simulations show that they increase and decrease together and that both populations can survive alone.

Two population interactions and learning environments

This paper is a technical paper in which we discuss ingredients relevant to the construction of interactive learning environments. As such, the actual use of the constructed material in a classroom setting is not discussed in this paper. Still it seems useful to summarise briefly some of the ideas that we have presented in previous publications on this issue. As mentioned before, several important ecological concepts are related to two populations models, such as communities, symbiosis, commensalism, parasitism, predation, herbivory, neutralism, amensalism, and competiton; they are used to introduce issues such as diseases, plagues and are input for biotechnology industry. Production of antibiotics, discovered after studies of an amensalism interaction between fungus *Penicillum* and bacteria is often quoted as an example.

In Salles & Bredeweg (2001) we discuss an educational learning route through a library of simulations modelling ecological phenomena. The main idea is to divide the scenarios (and thus the knowledge relevant to those scenarios) into six clusters of increasing complexity. Roughly, the idea is to work on individual populations in clusters C1 and C2, interactions between two populations in C3 and C4, and behaviour of communities (including the impact of environmental factors) in C5 and C6. Furthermore, the idea is that C1, C3 and C5 capture 'static' features (*e.g.,* what is a plant population and how does it differ from an animal population?) whereas C2, C4 and C6 represent the dynamic aspects (*e.g.,* what happens to the Prey when the size of the Predator increases?). Moving from one cluster to the next (and back if needed) means progressing along dimensions, such as *Order*, *Structural Change*, *Generalisation*, *Specialisation*, *Analogy* and *Inverse*. Each dimension facilitates specific learning opportunities. For example, amensalism is *analogous* to commensalism because one population is indifferent to the

other (not influenced by it). However, they differ in a particular feature: the positive versus negative influence on the other population. Learning assignments can be organised using these dimensions. In general, comparing simulations can be productive in problem solving activities. For example, an experiment with two interacting populations may involve the removal of one population and observing the behaviour of the remaining one. Suppose we have removed a population that was causing harm to a second one. If we do not know the effects of the second on the first population, then the relation can be represented as (?,–). A learner may now investigate three possible hypothesis: (+,–), (0, –) and (–, –), and run simulations with the known interactions from the library to discover the unknown relationship. Model inspection tools such as VisiGarp (Bouwer & Bredeweg, 2001) are important communication enablers in this respect[4].

Discussion and concluding remarks

Community behaviour can be seen as the result of a complex web of relationships and interactions between pairs of populations. Understanding such interactions constitutes an important part of ecological theory and practice. We have presented a set of qualitative simulation models that capture knowledge about the interactions between two populations. With these models it is possible to derive complex community behaviour from 'first principles' in ecology.[5]

Qualitative models can be used to support simulations in an interactive learning environment. They have the advantage that they allow for representing aspects that normally are hard to capture in numerical models, such as causal insights and the assumptions underlying a model. The latter is of particular interest for the work presented in this paper. Qualitative models force the model builder to explicate the details relevant to the interactions between populations. Initially, when reciprocal influences of two interacting populations are represented (*e.g.* as proportionalities), the reasoning engine generates all possible behaviours, because the situation is (qualitatively speaking) ambiguous. This means that for each interaction we have to specify exactly how that behaviour is different from 'just being ambiguous'. The qualitative approach enforces us to explicate the assumptions and constraints that must be true for interacting populations to show a certain type of behaviour. Articulating all that knowledge explicitly in simulation models is a major advantage of the work presented in the paper. The result provides an interesting workbench for learners to work with, while constructing their own understanding of interacting populations.

The quality of the models presented in this paper is

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[4] Pictures, such as shown in figure 1, 3 and 4, are generated using VisiGarp.
[5] The simulation software discussed in this paper can be downloaded from: http://web.swi.psy.uva.nl/projects/GARP/

guaranteed because of the fact that they have been developed in close collaboration with domain experts. Further validation of the usefulness of the models in a classroom setting is still in progress. However, previous studies (using complex simulation models of ecological phenomena) have shown results that are very encouraging in this respect (*cf.* Bouwer & Bredeweg, 2001). From a qualitative model construction viewpoint, there are many things to further explore in the future. One interesting next step is to work on representing more complex community behaviour using the simulations of interacting populations as building blocks.

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