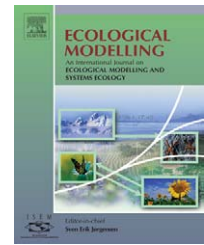


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The ants' garden: Qualitative models of complex interactions between populations

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ABSTRACT

Understanding interactions between populations is an important topic for research, management and education in ecology. However, a number of problems hamper the use of traditional modelling approaches when addressing complex systems involving three or more populations. In this paper we describe implemented qualitative models for improving understanding about the *ants' garden*, a complex system consisting of ants, their cultivated fungi, a virulent parasitic fungus that may attack the garden and bacteria that produce antibiotics against the parasitic fungus. These models are based on a qualitative theory of population dynamics and use models about symbiosis, commensalism, amensalism and parasitism to create the structure of the ants' garden. Simulations show the effects of changes in populations affecting the whole garden behaviour. Finally, we discuss the possibility of using a qualitative approach for building conceptual models of complex systems, grounding explanations on explicit representations of the causal influences, implementing easy to change assumptions, testing different hypotheses and complementing numerical models.

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1. Introduction

Because few organisms cultivate their own food, fungus-gardening by ants is considered to be a major breakthrough in evolution. It is a symbiosis in which organisms of two different species (ants from the family *Formicidae* and fungi mostly from the family *Lepiotaceae*) benefit each other and creates a system that can successfully survive in a number of different environments, being the dominant herbivores in the Neotropics. Recent studies (Currie et al., 1999a,b) showed that the *ants' garden* is far more complex than initially understood. A third species, the specialized garden parasite fungi of the genus *Escovopsis* is often involved and may destroy the system, by attacking the cultivated fungi. However, it almost never hap-

pens because ants carry on their body colonies of bacteria (genus *Streptomyces*) that produce antibiotics effective to control the growth of *Escovopsis*. Therefore, the system consists of four species and of complex balance of interactions in which eventually the ants' garden survives. The basic configuration of the ant's garden is shown in Fig. 1.

Interactions between populations have been a hot topic in ecological theory and practice. Competition, for instance, is still seen as a driving force for shaping biological communities. However, traditional modelling approaches, mostly based in differential and difference equations, are limited in many aspects. In general, they are difficult to build, very hard to calibrate and almost impossible for non-experts to understand their result. Such models are 'black boxes', that is, they have

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no a clear representation of the system structure and cannot explain how a system works (Gillman and Hails, 1997).

Applied to more complex systems, the predictive capacity of numerical population models may be jeopardized by other problems. It has been shown that even simple mathematical models may produce complex trajectories, with stable points, cycles and chaotic behaviour (cf. May, 1974, 1976). For example, modelling interactions among populations with ordinary differential equations, Gilpin (1979) demonstrated that chaos can be observed when there are at least three populations. Cyclic behaviour has been observed in many populations, but the existence of chaotic behaviour in natural populations is still an open question (e.g., May, 1974; May and Oster, 1976).

Qualitative reasoning models (Weld and de Kleer, 1990) may play an important role in this discussion, particularly for representing the structure of the system and grounding causal explanations about the system behaviour in this structure. We here describe models about the ants' garden developed for improving understanding about this complex system, implemented on the top of models about single population dynamics (Salles and Bredeweg, 1997) and interactions between two populations (Salles et al., 2003). These models are 'simpler' than the complex mathematics used to represent population and community dynamics but powerful enough to support useful conclusions about the system behaviour.

We start presenting the ants' garden and some questions we expect our models to answer (Section 2), and then discuss related work on building qualitative models about populations (Section 3). The model building effort (Section 4), the resultant models (Section 5) and simulations with two models (Section 6) are presented next. Finally, we comment related work (Section 7) and discuss the potential of qualitative modelling approaches for representing complex systems with more than two populations and how they can complement current techniques used in ecological modelling (Section 8).

2. How does the ants' garden system work?

The ants' gardens have been thought to be 'monocultures' free of microbial parasites, but it has been discovered that they are hosts of specialized garden parasites belonging to the genus *Escovopsis*. Currie et al. (1999b) noted that these fungi are only known from attine gardens and that they are found in many attine nests. In the absence of the ants, rapidly and almost invariably *Escovopsis* overgrow the garden. Instead of multiple contaminants, after removal of tending ants, gardens with

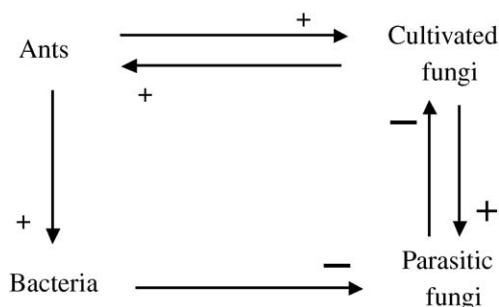


Fig. 1 – The ant's garden: positive and negative interactions.

endemic *Escovopsis* were only overgrown by this fungus. Actually, even in the presence of ants *Escovopsis* may overgrow gardens, both in the field and in laboratory (Currie et al., 1999b).

What factors may control *Escovopsis* growth and keep the ants' garden working? Further studies discovered a third mutualist, bacteria of the genus *Streptomyces*. These bacteria have been largely used in the pharmaceutical industry to produce antibiotics for human use. Currie et al. (1999a) demonstrate that they produce antibiotics that specifically suppress the growth of *Escovopsis*. Further studies indicate that *Streptomyces* produce metabolites (vitamins, amino acids) that may enhance the growth of the cultivated fungi (Currie et al., 1999a).

A modelling approach may provide a representation of the system structure to support explanations about why the system behaves as it does. Models are intellectual tools that give a 'simplified' picture of reality. In some way, models reflect our knowledge about a system, and provide formal representations of this understanding so that they can be assessed by members of the scientific community (Jørgensen and Bendoricchio, 2001).

Models designed to improve the understanding of the system are also called conceptual models. According to Grimm (1994), conceptual models should be understandable, manageable and allow full exploration. These kinds of models can be used for supplying a 'conceptual framework' for a research program and for proposing and testing hypotheses, that is, to demonstrate the 'consequences of what we believe to be true'.

The objective of the work described here is to build models to improve learners understanding of the ants' garden. The models described here should be able to answer questions such as *What are the mechanisms, at the population level, that keep the ants' garden functioning, even in the presence of parasitic fungi?* As shown in the following sections, we explore the causal dependencies in interactions between the four populations to provide answers for this question.

3. Modelling approaches to multi-species communities

Theoretical population ecology became a well-established discipline during the 20's and 30's by Lotka, Volterra, Gause and others. These authors have developed mathematical approaches both to field and to experimental population ecology that still are references for modelling population dynamics and interactions between populations (Kingsland, 1991). Although powerful and elegant, differential equations pose a number of constraints on the way knowledge is represented, and require good quality data. Given that data about ecological systems are often difficult to obtain and available knowledge is incomplete, qualitatively expressed, building mathematical ecological models is thus not an easy task. Nevertheless, most of the ecological modelling approaches are based on mathematical equations.

In spite of the wide acceptance of mathematical population ecology (cf. May, 1976), during the 1970s these models received some criticisms: they assume a deterministic approach to systems that are affected by stochastic factors; they are not adequate to describe the behaviour of certain species; they

oversimplify the problems and so on. Moreover, it has been shown that the very simplest non-linear difference equation can possess a rich spectrum of dynamic behaviour, from stable points to stable cycles and to a regime in which the behaviour, although fully deterministic, is in many aspects “chaotic” (May, 1976). Further studies on this topic are not conclusive and whether or not natural populations present chaotic behaviour is still an open question (Godfray and Blythe, 1990).

Derived from population dynamics, research on community dynamics has been assuming that all the species in a community were fluctuating around a stable equilibrium of densities of the different populations. It was accepted that more complex biological systems (defined in terms of the number and nature of the individual links in the trophic web) would become more stable (defined by the tendency of returning to the equilibrium after small perturbations). Investigations described by May (1973) did not support this idea and fuelled a discussion about whether or not complexity and stability are in fact coupled in biological communities.

It is interesting to build models that predict behaviours that were not observed in nature. However, the fact that simple and deterministic equations can possess dynamical trajectories which look like random noise has disturbing practical implications for the analysis and interpretation of biological data, as discussed by May and Oster (1976). Being black box models (Gillman and Hails, 1997), the use of these approaches is not very helpful to improve understanding about the structure and behaviour of ecological systems.

Alternative approaches and conceptual models are urgently required to enhance understanding about complex ecological systems. Qualitative reasoning models (Weld and de Kleer, 1990) are an interesting option in a situation like this, providing representations of relevant concepts when mathematical approaches in general are not good options or when the lack of good quality numerical data hampers their application. Some basic concepts of qualitative reasoning models are presented in the next section.

4. Qualitative reasoning and population ecology models

In this modelling effort, we adopted the ontology provided by the qualitative process theory (Forbus, 1984). This theory defines a simply notion of physical processes that is a useful language to write domain theories about dynamics. Accordingly, *processes* are assumed to be the only mechanism that may cause changes in the system. Two modelling primitives are used to represent the effects of processes: *direct influences* ($I+$; $I-$) and *qualitative proportionalities* ($P+$; $P-$).

These modelling primitives have both a mathematical and a causal interpretation. The mathematics of direct influences and proportionalities can be summarized as follows. Direct influences define the derivative of influenced quantities. Thus, for example, the expression $I+(Y, X)$ reads $dY/dt = (\dots + X \dots)$. If this is the only direct influence on Y , then its derivative will take the value X and, if $X > 0$, it will increase by an amount equals X . Compared to differential equation models, Y plays the role of a state variable and X is the rate of the process. Negative direct influences have similar inter-

pretation, except that the rate is subtracted from the state variable.

Qualitative proportionalities carry much less information than direct influences. According to Forbus (1984), $P+(A, Y)$ represents a situation in which there exists a function that determines A and is increasing monotonic (that is, strictly increasing) in its dependence on Y . In algebraic notation, this can be represented as $A = f(\dots, Y, \dots)$. In other words, if $P+(A, Y)$ is the only influence on the quantity A , then when Y is changing (increasing or decreasing), A is also changing, in the same direction. Negative proportionalities are defined in the same way, except that the function is decreasing monotonic.

Combining more than one direct influences or qualitative proportionalities is called *influence resolution*. If their relative strength is known, there is no ambiguity. If not, either the modeller should include extra knowledge or the reasoning engine will try all the possible combinations, increasing the number of states in the simulation.

Causality is represented in both direct influences and proportionalities as flowing in one direction: for example, in both expressions $I+(Y, X)$ and $P+(Z, W)$, the quantities X and W cause changes, respectively, in Y and Z , and not the contrary. Combinations of direct influences and proportionalities suffice for building causal chains. For example, if $I+(Y, X)$ and $P+(A, Y)$ and the process is active, then Y increases by an amount equals to X and given that Y is increasing, A will increase as well. A number of examples of this causal reasoning will be given below.

Using the ontology provided by the qualitative process theory, we implemented a qualitative theory of population dynamics, used as the basis for representing the succession in the communities of the Brazilian Cerrado vegetation (Salles and Bredeweg, 1997), interactions between populations (Salles et al., 2003) and now to implement models about the ants' garden.

The starting point of the qualitative domain theory of population dynamics is the equation:

$$\begin{aligned} \text{Number_of}_t = & \text{Number_of}_{t-1} \\ & + (\text{Born} + \text{Immigrated}) - (\text{Dead} + \text{Emigrated}) \end{aligned}$$

where *Number_of* is the number of individuals in the population at the time points t and $t - 1$, and *Born*, *Immigrated*, *Dead* and *Emigrated* are the rates of the basic processes of natality, immigration, mortality and emigration. The qualitative representation of this equation is:

$$I+ (\text{Number_of}, \text{Born}); \quad I+ (\text{Number_of}, \text{Immigration});$$

$$I- (\text{Number_of}, \text{Dead}); \quad I- (\text{Number_of}, \text{Emigration}).$$

In order to capture the idea that there is a feedback loop involving these quantities, so that when the population size increases (or decreases), the rates of the basic processes also change (except immigration because it is seldom influenced by the population size), the following three proportionalities were implemented:

$$P+ (\text{Born}, \text{Number_of}); \quad P+ (\text{Dead}, \text{Number_of});$$

$$P+ (\text{Emigration}, \text{Number_of}).$$

For implementing the domain theory we adopt the *compositional modelling* approach (Falkenhainer and Forbus, 1991). Accordingly, domain knowledge is encoded as stand alone partial models called *model fragments*. A model fragment often contains information about objects, relations with other objects, quantities and their possible values, inequality statements, causal dependencies and descriptions of situations and processes. Model fragments are automatically combined by the reasoning engine in order to compose a running model. The model building activity is, in fact, the work of building a *library* of model fragments. These model fragments can be reused, so that the library, in general, supports the construction of more than one model, scaling up the level of complexity (considering the number of processes and state variables included in the model). A special type of model fragment is the *initial scenario*, used to start a simulation. A scenario contains a partial description of the system, including objects, relations, dependencies and the initial values of relevant quantities.

The models described here were implemented in the domain independent qualitative simulator GARP (Bredeweg, 1992). Associated to GARP we used the graphical tool VisiGarp (Bouwer and Bredeweg, 2001) to inspect the running models and the simulations.

Given an initial scenario, the library, and a set of model fragments specifying domain independent transition rules, GARP produces a simulation. This is done by selecting from the library the model fragments that mention the entities and fit to the conditions stated in the initial scenario. From the initial scenario, one or more initial states are created. A *qualitative state* is a unique description of the structure of the system combined with a distinctive set of values associated to the quantities of interest, described by a particular subset of model fragments. Next, GARP checks the conditions of the system in that state and proceeds to the influence resolution of direct influences and proportionalities. As a result, new conditions are defined and GARP goes through the library again, selecting a new set of model fragments that are consistent with the new conditions of the system. In the description of this new state, some model fragments active in the previous state may continue to hold, some may be removed and new ones may be included. Details of GARP and the reasoning process can be found in Bredeweg (1992), Salles and Bredeweg (2003, in press) and in Bredeweg et al. (in press).

The backbone of GARP models is the description of the entities involved in the model and definitions of how they are related. For example, a model may include the entities ‘population’ and ‘biological entity’ and their relation may be defined by the statement ‘consists of’. In this case, the structure of the model can be described as ‘population consists of biological entity’. Relevant properties of the entities are represented as quantities. For example, the size of the entity ‘population’ can be represented by the quantity *Number_of*.

Numerical values of quantities are abstracted in order to represent just their most relevant qualitative states. In qualitative models, these values are included in a set called *quantity space* (Forbus, 1984). Any quantity value in a GARP model is characterized by the tuple (*magnitude, derivative*). The former gives an idea of the ‘size’ of the quantity and the latter defines its direction of change. We may say that the magnitudes of *Number_of* assume qualitative values from the quantity space

{*zero, normal, maximum*}. The magnitudes of birth rate (*Born*) and death rate (*Dead*) are included in the quantity space {*zero, plus*}. Derivatives of all the quantities have quantity space {*minus, zero, plus*} meaning that the quantity is decreasing, stable or increasing, respectively.

As typically occurs in Artificial Intelligence, entities are represented by using a subtype (*isa*) hierarchy. In this *isa hierarchy* entities placed below in the hierarchy inherit attributes from the entities above. For example, the models described in this paper include entities such as ‘population’ and, below it, ‘ants’. Assuming that ‘ants’ *isa* ‘population’, GARP associates to ‘ants’ the quantity *Number_of* and its quantity space. This is a powerful way of encoding knowledge: a domain theory about population dynamics defined for the entity ‘population’ can be associated to the entities involved in the ants’ garden.

Entities may be physical objects or conceptual objects. Concepts are also organized in subtype hierarchies. The models described here include conceptual entities such as ‘assumptions’. Examples are the ‘operating assumptions’ and the ‘simplifying assumptions’. *Operating assumptions* play an important role in defining a perspective for approaching the system. For instance, if the operating assumption ‘closed population’ is assumed, as done for the models described here, then only natality and mortality processes are considered. *Simplifying assumptions* do not change the structure of the system but simplify the simulations, because they reduce the number of ambiguities and the number of states in a simulation. For example, models about parasitism may include *correspondences* (Bredeweg, 1992) between the population size and the strength of its effect on the other population. This way, *Number_of = maximum* corresponds to an effect with maximum strength (see below).

The simulation run in GARP can be inspected with the visualizing tool VisiGarp (Bouwer and Bredeweg, 2001). The *state graph* (or behaviour graph) shows the set of states and state transitions produced during the simulation. A sequence of states is called a behaviour path. It is possible to identify a set of behaviour paths in the state graph. The state where a behaviour path finishes is called an *end state*. Other aspects of the simulation can be explored with VisiGarp. Worth to mention here are the dependencies and the so-called value history diagram. The former presents the causal model, a diagram with the quantities and the active dependencies (direct influences, proportionalities, correspondences and inequalities) relating them in each state. The value history diagram represents the values of magnitude and derivative each quantity assumes in each state during the simulation. Each sequence of states and state transitions constitutes a behaviour path; it is possible to follow the changes a quantity goes through during the simulation. A number of examples of these features are presented in the sections below.

In the next section, we present the models about interactions between populations used for implementing the ants’ garden.

5. The ants’ garden models

Different types of interactions between populations can be described according to the effects each population causes on

Table 1 – Interactions between the four populations involved in the ants' garden

	Ants	Cultivated fungi	Parasitic fungi	Bacteria
Ants	**	+	?	+
Cultivated fungi	+	**	+	?
Parasitic fungi	?	–	**	?
Bacteria	?	+	–	**

The sign refers to the effects of the population in the row on the population in the column. For example: the fourth row reads as bacteria having an unknown influence (?) on the ants, a positive effect (+) on cultivated fungi, and a negative effect (–) on parasitic fungi. The symbol (**) indicates self-interaction.

the growth of the other population (positive, neutral or negative) by combining the signs, respectively {+, 0, –} (Odum, 1985). Following this author, we use [(predator, prey) = (+, –)] to represent, for example, predation. The predator increases due to the positive influence (+) from the prey, while the latter decreases due to the negative influence (–) from the predator.

Table 1 presents the relationships between the four species involved in the ants' garden system, as inferred from Currie et al. (1999a,b).

The relations between ants and cultivated fungi, and between cultivated fungi and parasitic fungi are clearly defined in the table. However, some interactions are only partially defined. They are: [(ants, bacteria) = (? , +)]; [(bacteria, parasitic fungi) = (? , –)] and [(bacteria, cultivated fungi) = (? , +)]. For the sake of simplicity, we assume that these relations are unidirectional, that is, both ants and bacteria are not affected by the other populations. Therefore, we define the following relations as the minimum set of interactions required to model the ants' garden:

- (a) [(ants, cultivated fungi) = (+, +)];
- (b) [(parasitic fungi, cultivated fungi) = (+, –)];
- (c) [(ants, bacteria) = (0, +)];
- (d) [(bacteria, parasitic fungi) = (0, –)];
- (e) [(bacteria, cultivated fungi) = (0, +)].

Salles et al. (2003) describe six models of interaction types between populations, defined by all the possible combinations of the signs {+, 0, –}. According to Odum (1985), these combinations can be used to represent nine types of interactions, given that some pairs apply to more than one type of interaction. For example, (+, –) can be used to represent predation, herbivory and parasitism. In order to implement the ants' garden models, we took from Salles et al. (2003) the following models: symbiosis (a), parasitism (b), commensalisms (c, e) and amensalism (d). Recently, these models have been slightly adapted following discussions with experts. For details see Bredeweg and Salles (in press).

The library for the ants' garden models consists of 33 model fragments. Three model fragments are used for a general definition of population. The model fragment 'Population' defines the relation between a set of things (population) and a biological entity (species): 'population consists of species'. The quantity *Number_of* is introduced and associated to population. This model fragment has two subtypes: 'Existing population' and

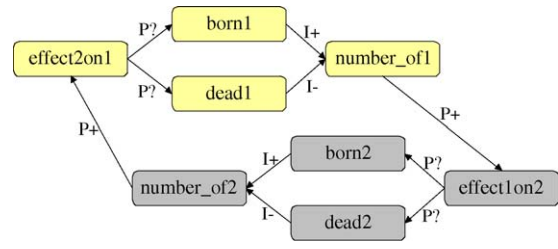


Fig. 2 – Base model for two interacting populations models (Salles et al., 2003).

'Non-existing population'. In the former, *Number_of* is greater than zero and, in the latter, equal to zero.

The assumption that only natality and mortality processes may be active is implemented by the model fragment 'Assume_open_population'. As this assumption applies to all interactions, only the model fragments 'Natality' and 'Mortality' are included in the ants' garden models.

The models of interactions are specifications of the basic architecture depicted in Fig. 2.

As shown in Fig. 2, the effect one population can cause on the other is represented by the quantity *Effect*. The effects of population1 on population2 and vice versa are represented, respectively, by *Effect1on2* and *Effect2on1*. These quantities are renamed to better express each interaction. For example, *Benefit* or *Supply* in positive interactions and *Consumption* or *Pollution* in negative interactions. The relation between effect and the size of the influencing population is modelled by the proportionality $P + (Effect, Number_of)$.

This option for an intermediate quantity (*Effect*) as an alternative for creating an influence directly from *Number_of* to the influenced population increases the representational capacity of the models, as it allows for modelling a situation in which *Effect* either corresponds or not to the size of the population that produces the effect. For example, the ants interact both with cultivated fungi and with bacteria. Each interaction is modelled by a specific quantity *Effect* and their values can be different.

Given that only processes may change the population size, in the ants' garden models a population influences the other population via the basic processes of natality and mortality. A positive interaction, for example, can be implemented as increasing the birth rate, $P + (Born, Effect)$, decreasing the death rate, $P - (Dead, Effect)$, or both at the same time. Similarly, negative interactions can decrease the birth rate; increase the death rate or both.

Each interaction is typically modelled by using five model fragments: a model fragment that defines general aspects of the interaction, and four subtype model fragments to implement detailed knowledge. Among them, one model fragment specifies details of the interaction; two model fragments define the absence of each population; and one model fragment defines some simplifying assumptions for the interaction. Extra model fragments may be used to implement extra assumptions for the interactions. Details of each interaction included in the ants' garden models are described below.

To model parasitism, a set of five model fragments are used. The most general is 'Parasitism', which introduces the two

populations, being population1 the parasite and population2 the host, and the quantities *Supply* (the effect of the host on the parasite) and *Consumption* (the effects of parasite on the host). A directed correspondence (Bredeweg, 1992) establishes that the magnitude of *Supply* takes the same values as the magnitude of *Number_of2*. The relation between the values of *Consumption* and *Number_of1* is represented in the same way.

The model fragment 'Parasitism interaction' implements the effects of the interaction: it establishes that *Supply* increases *Born1* and decreases *Dead1*, while *Consumption* increases *Dead2*. This model fragment also assumes that both the magnitude and the derivative of *Supply* have to be greater than or equal to, respectively, the magnitude and the derivative of *Consumption*. This way, consumption is less than or, at most, equal to supply and there is no food shortage for the parasite.

The conditions for parasite and host populations to go extinct are defined, respectively, by the model fragments 'Parasitism without parasite' and 'Parasitism without host'. The former sets no constraints or consequences for the host population due to the disappearance of the parasite population. However, we assume that the parasite cannot exist without the host: if *Number_of2* goes to zero, then *Number_of1* will do the same. Finally, simplifying assumptions for this interaction are encoded in the model fragment 'Parasitism assumptions': directed correspondences establish that the derivatives of *Born* and *Dead* take the value of the derivative of *Number_of*. This assumption reduces the number of possible combinations (for example, *Born* increasing, *Dead* decreasing and *Number_of* increasing), and therefore reduces the size of the simulations.

Symbiosis is also modelled by five model fragments. 'Symbiosis' is the most general one, and introduces the two populations (1 and 2) and the quantities *Benefit1* and *Benefit2*. As in parasitism, direct correspondences establish that magnitudes of *Benefit* take the same magnitudes of *Number_of* in both populations.

The model fragment 'Symbiosis interaction' defines how the effects are implemented: in both populations, *Benefit* increases *Born* and reduces *Dead*. This model fragment also implements correspondences establishing that the maximum value of *Benefit1* corresponds to the maximum value of *Benefit2*, and that the derivatives of the two benefits correspond. These assumptions are useful to reduce ambiguities during the simulation. The conditions for the absence of each population are represented in two model fragments, 'Symbiosis without symbiont1' and 'Symbiosis without symbiont2'. Given that we assume the symbiosis as being obligatory for both ants and cultivated fungi (they cannot survive alone, according to Currie et al. (1999a)), when *Number_of1* is zero, *Number_of2* will be also zero, and vice versa. Finally, the model fragment 'Symbiosis assumptions' sets for this interaction the same simplifying assumptions defined for parasitism.

Commensalisms are modelled by a set of eight model fragments. 'Commensalisms', the most general one, introduces the two populations and the quantity *Benefit*, to represent the influence of population1 on population2. This quantity corresponds to *Number_of1* and their maximum values are assumed to be equal.

The model fragment 'Commensalisms interaction' defines that *Benefit* increases *Born2* and reduces *Dead2*. Our under-

standing that bacteria disappear from the ants' garden if they do not receive the benefit from the ants is captured in the model fragment 'Commensalisms without producer'. It establishes that if *Number_of1* is zero, then *Number_of2* also should go to zero. The model fragment 'Commensalisms without affected' sets no constraints or consequences for population1 due to the disappearance of population2. Finally, as in parasitism and symbiosis, simplifying assumptions involving *Number_of*, *Born* and *Dead* are implemented by the model fragment 'Commensalisms assumptions'.

Three model fragments implement constraints on the strength of the influence of population1 on population2. 'Commensalisms effects magnitude1' establishes that only when *Benefit* has value *maximum*, *Number_of2* can go to *maximum*. 'Commensalisms effects magnitude2' establishes that if the magnitude of *Benefit* is *normal*, then the magnitude of *Number_of2* has to be below *maximum*. Finally, 'Commensalisms high impact' implements the 'commensalisms high impact' assumption, which establishes that the value of *Number_of2* always corresponds to the values of *Benefit*. This assumption is more restrictive because the value of the former is completely determined by the latter. As a consequence, the number of states in a simulation is reduced.

Finally, amensalism is implemented with eight model fragments in the same way as commensalisms. The model fragment 'Amensalism' introduces the two populations and the quantity *Pollution* to represent the effect of population1 on population2. It is also assumed that the maximum value of *Pollution* corresponds to the maximum value of *Number_of1*. The model fragment 'Amensalism interaction' defines that *Pollution* decreases *Born2* and increases *Dead2*. The model fragments 'Amensalism without producer' and 'Amensalism without affected' set no constraints or consequences for any population due to the disappearance of the other population. The same simplifying assumptions already described for the other three interactions are implemented for amensalism by the model fragment 'Amensalism assumptions'.

As in commensalisms, three model fragments implement details about the strength of the amensalism interaction: 'Amensalism effects magnitude1' establishes that if *Pollution* has value *maximum*, then *Number_of2* has value zero; 'Amensalism effects magnitude2' determines that if *Pollution* has value *normal*, then *Number_of2* has to be smaller than *maximum*; and 'Amensalism effects magnitude3' establishes that if *Pollution* has value zero, then *Number_of2* can assume any value.

It is important to mention that these magnitude assumptions implemented in commensalisms and amensalism do not produce unknown or unexpected behaviours, but only control the level of details represented in the simulations. For example, when the 'commensalisms high impact' assumption is not introduced in the initial scenario, the simulation has more states to express fundamentally the same behaviours, and most of these states show different combinations of derivative values of the quantities. These results are correct, but superfluous, as they do not give additional insights to the understanding of the system.

In the next section we describe three simulations obtained with two models of the ants' garden.

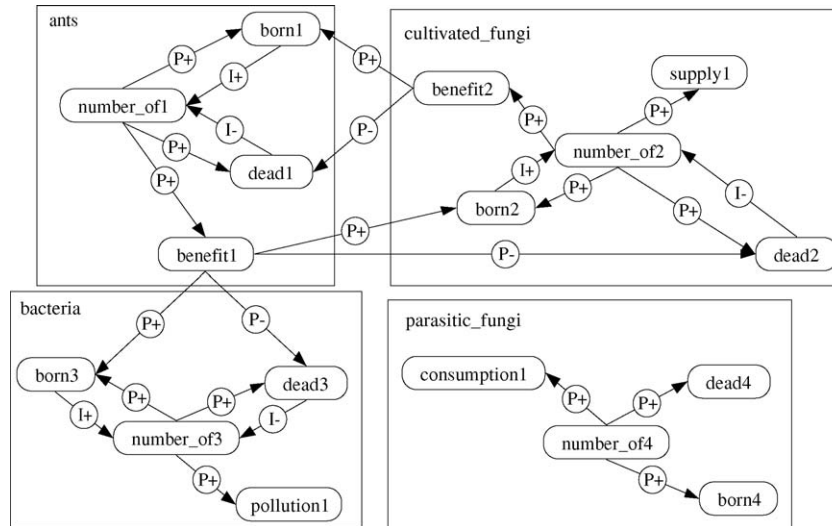


Fig. 3 – Causal dependencies involving four populations (four interactions) in state 3 of simulation 1.

6. Simulations with the ants’ garden models

As mentioned above, building qualitative models is actually building libraries of model fragments and initial scenarios. From such libraries, often the reasoning engine can automatically build a number of simulation models exploring different aspects of the encoded domain knowledge.

Following the suggestions of Salles and Bredeweg (1997), the ants’ garden library was built incrementally. Starting with simulation models about the symbiosis between ants and cultivated fungi, we included parasitism between cultivated and parasitic fungi and commensalisms to express the relation between ants and bacteria. Finally, we introduced commensalisms between bacteria and cultivated fungi. Adequate initial scenarios can retrieve simulations of each of these steps.

Simulations involving two models of the ants’ garden will be shown in this section. The first model consists of four populations linked by four interactions. Only the relation between bacteria and cultivated fungi is not considered. Two simulations are run with this model, showing the ants’ garden without the parasitic fungi and the four populations with initial values set to normal, with unknown derivatives. The second model implements the fifth interaction, representing the interaction between bacteria and cultivated fungi. A simulation with this model will show the outcomes of the four populations with initial values set to normal, with unknown derivatives. In both models, the ‘commensalisms high impact’ assumption is included. Details of each simulation are presented below.

6.1. Simulation 1

The initial scenario describes four populations and four interactions between them, with the initial values of Number_of ants, cultivated fungi and bacteria set in (normal, ?), that is, magnitude normal and derivative unknown, while Number_of

parasitic fungi is (zero, ?). Three initial states are derived from the initial scenario. While the parasitic fungi are stable in all these initial states, the other three populations may be decreasing (state 1), stable (state 2) and increasing (state 3). The causal model, as it appears in state 3, is presented in Fig. 3.

The full simulation produces eight states. The state graph of this simulation and the values (magnitude and derivative) of the state variables Number_of in these states are shown in Fig. 4.

The state graph shows six end states, that is, states in which the behaviour path stops: [2, 4, 5, 6, 7, 8]. The behaviours observed in these end states are, respectively, the following: the three populations are stable in the value normal (2); or in the value maximum (4); cultivated fungi is stable in normal while the other two populations are stable in maximum (5); ants and bacteria are stable in normal and cultivated fungi is stable in maximum (6); bacteria is extinct (7); and, finally, the whole system is extinct (8). Behaviours expressed by the system and the six possible behaviour paths are shown in Table 2.

The results of the simulation with this model were as we would expect for an ants’ garden free of parasitic fungi: different states of coexistence of the three populations; and, as we assume an obligatory symbiosis between ants and cultivated fungi, either only the bacteria is extinct or the whole garden is extinct. Worth to mention is that natality and mortality of parasitic fungi are not active because this population has magnitude zero, a ‘Non-existing population’. In this case, no direct

Table 2 – Behaviours and behaviour paths expressed by the ants’ garden in simulation 1

Behaviour of the system	Behaviour paths
Coexistence of the three populations	[2], [3 → 4], [3 → 5] and [3 → 6]
Extinction of bacteria	[1 → 8]
Extinction of the whole system	[1 → 7]

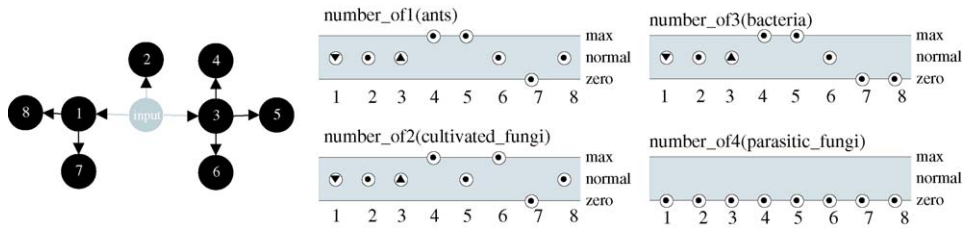


Fig. 4 – State graph and value history of the quantities *Number_of* of the four populations (four interactions) in simulation 1.

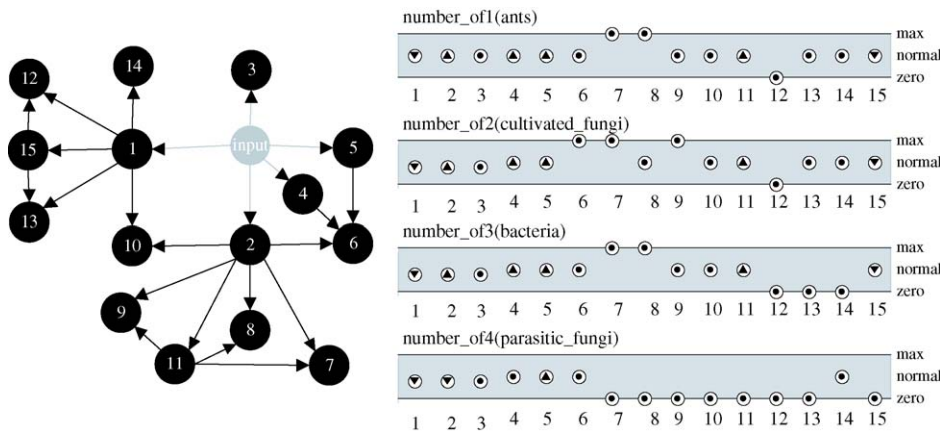


Fig. 5 – State graph and value history of the quantities *Number_of* of the four populations (four interactions) in simulation 2.

influences are affecting *Number_of* (see Fig. 3). The same configuration appears when a population goes extinct during the simulation (for example, bacteria in state 8). These examples illustrate one of the most interesting features of qualitative reasoning models: the possibility of including into or removing from the model structural elements during a simulation.

6.2. Simulation 2

The second simulation with this model starts with an initial scenario which assigns to *Number_of* the value (*normal*, ?), that is magnitude normal and derivative unknown, for all the populations. From this initial scenario, five initial states are produced. The magnitudes of the state variables are the same (*normal*), but their derivatives are different: all the populations are decreasing (state 1); parasitic fungi is decreasing, while the others are increasing (state 2); all the populations are stable (state 3); parasitic fungi is stable and the others are increasing (state 4); and all the populations are increasing (state 5).

The full simulation consists of 15 states. The state graph and the value history showing magnitudes and derivatives of the state variables *Number_of* ants, cultivated fungi, bacteria and parasitic fungi are depicted in Fig. 5.

The simulation produces nine end states: [3, 6, 7, 8, 9, 10, 12, 13, 14]. The behaviours expressed in these end states are, respectively, the following: the four populations are stable with value *normal* (3); ants, bacteria and parasitic fungi are stable in *normal*, and cultivated fungi is stable in *maximum* (6); ants, cultivated fungi and bacteria are stable in *maximum*, and parasitic fungi is extinct (7); ants and bacteria are stable in *maximum*, cultivated fungi is stable in *normal*, and parasitic

fungi is extinct (8); ants and bacteria are stable in *normal*, cultivated fungi is stable in *maximum*, and parasitic fungi is extinct (9); ants, bacteria and cultivated fungi are stable in *normal*, and parasitic fungi is extinct (10); ants and cultivated fungi are stable in *normal*, parasitic fungi and bacteria are extinct (13); bacteria is extinct (14); and, finally, all the garden is extinct (12).

The 17 possible behaviour paths are shown in Table 3.

This simulation shows a rich variety of behaviours expressed by the garden, according to the implemented assumptions: coexistence of the four populations, with different population sizes; extinction of parasitic fungi and stabilization of the other three populations in different values; extinction of bacteria and of parasitic fungi; extinction of the bacteria; and the extinction of the garden. As in the previ-

Table 3 – Behaviours and behaviour paths expressed by the ants' garden in simulation 2

Behaviour of the system	Behaviour paths
Coexistence of the four populations	[3], [4 → 6], [5 → 6] and [2 → 6]
Extinction of parasitic fungi and coexistence of the other populations	[1 → 10], [2 → 7], [2 → 11 → 7], [2 → 8], [2 → 11 → 8], [2 → 9], [2 → 11 → 9] and [2 → 10]
Extinction of parasitic fungi and bacteria	[1 → 13] and [1 → 15 → 13]
Extinction of bacteria	[1 → 14]
Extinction of the whole system	[1 → 12] and [1 → 15 → 12]

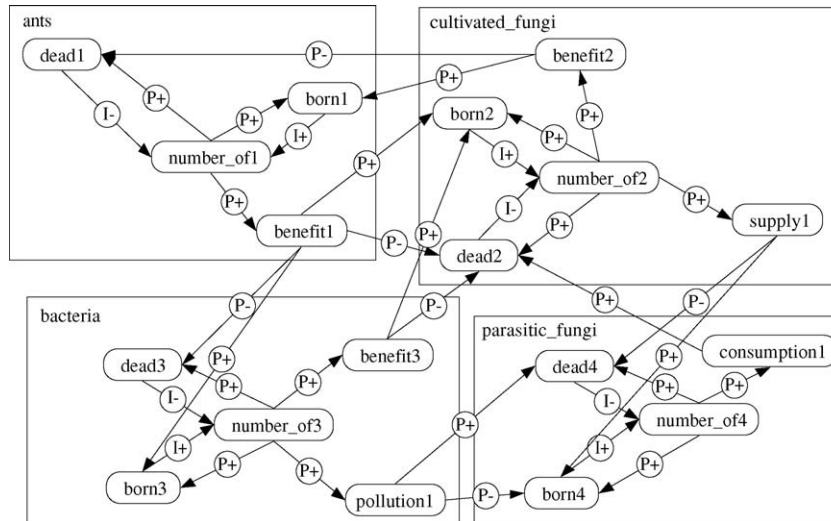


Fig. 6 – Causal dependencies involving four populations (five interactions) in state 5 of simulation 3.

ous simulation, ants and cultivated fungi are always present, except when the whole garden disappears.

6.3. Simulation 3

For this simulation we used a model that includes commensalisms to represent the fifth interaction, namely between bacteria and cultivated fungi. The initial values of all the state variables *Number_of* are set in *(normal, ?)*. GARP derives five initial states, with the same values observed in the five initial states of simulation 2. The causal dependencies of this model, as they appear in state 5, are depicted in Fig. 6. Note the effects of bacteria on the other populations, represented by two quantities: *Pollution* (which affects parasitic fungi) and *Benefit* (which affects cultivated fungi).

The whole simulation consists of 10 states. The state graph and the values of magnitudes and derivatives of *Number_of* of the four populations are depicted in Fig. 7.

The state graph shows that the six end states of the simulation are [3, 4, 5, 6, 7, 9]. The behaviours expressed in these end states are, respectively, the following: the four populations are stable with value *normal* (3); ants, bacteria and cultivated fungi are in value *(normal, +)* and parasitic fungi is stable in *normal* (4); the four populations are in value *(normal, +)* (5); ants, bacteria and cultivated fungi are stable in *maximum*, and parasitic fungi is extinct (6); ants, bacteria and cultivated fungi are stable in *normal*, and parasitic fungi is extinct (7); all the garden is extinct (9).

The behaviours expressed by the garden and the nine possible behaviour paths are shown in Table 4.

The inclusion of the interaction between bacteria and cultivated fungi increased the possibilities of coexistence, as shown in states 4 and 5. Also, the extinction of the bacteria population was not observed, except along with the other three populations. This can be explained by the assumption implemented by the model fragment ‘Commensalisms without producer’ (see Section 5): when bacteria go to value zero, then cultivated fungi also should assume the value zero. However, for the latter to be true, the ants should assume the

value zero as well. This prevents the bacteria to be extinct alone.

7. Related work

Given the difficulties of using mathematical models when knowledge is incomplete or numerical data have no good quality or simply do not exist, a number of authors tried alternative approaches for modelling multi-species community dynamics. Some of these works are commented in this section.

Noble and Slatyer (1980) and Moore and Noble (1990, 1993) proposed an approach for building qualitative models about the dynamics of communities subject to recurrent disturbance (such as fire). This approach is based on a small number of attributes of the plant’s life history (vital attributes), which can be used to characterise the potentially dominant species in a particular community, under different types and frequencies of disturbance. Simulations typically produce a replacement sequence which depicts the major shifts in composition and dominance of species which occur following a disturbance. These models differ from ours in many aspects. They describe the replacement sequence, but cannot provide causal explanations for changes in the system. Also, these models rely on

Table 4 – Behaviours and behaviour paths expressed by the ants’ garden in simulation 3

Behaviour of the system	Behaviour paths
Stable coexistence of the four populations	[3]
Three populations increasing and parasitic fungi stable	[4]
The four populations increasing	[5]
Extinction of parasitic fungi and coexistence of the other populations	[2 → 6], [2 → 8 → 6], [1 → 7] and [2 → 7]
Extinction of the whole system	[1 → 9] and [1 → 10 → 9]

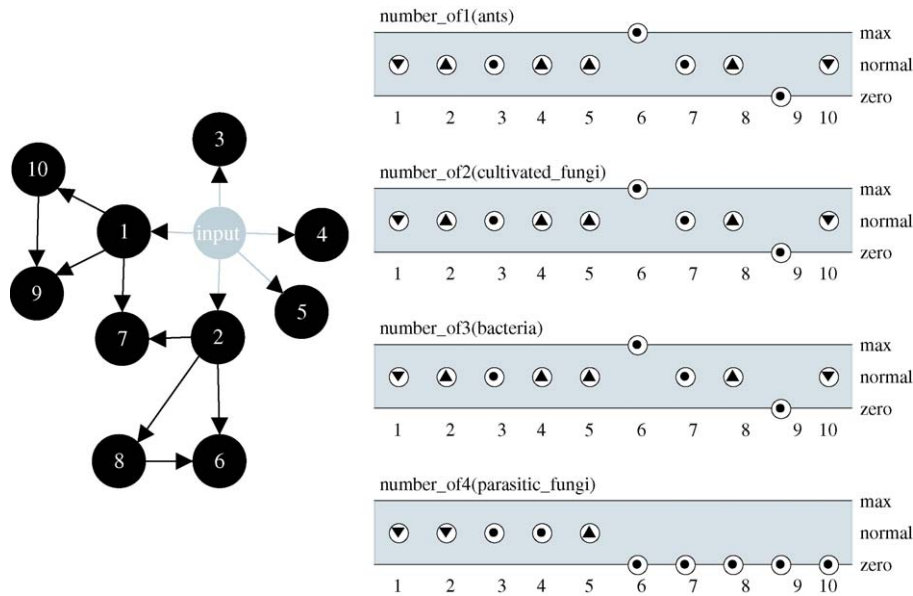


Fig. 7 – State graph and value history of the quantities *Number_of* of the four populations (five interactions) in simulation 3.

mathematical simulations for calculating changes in population sizes, while our representation is based only in qualitative knowledge, including magnitudes and derivatives of the quantity values.

State-transition modelling is often used to describe community dynamics. For example, McIntosh (2003) presents a rule-based modelling language to describe succession in communities stressed by fire and grazing using this paradigm. Pivello and Coutinho (1996) also describe a state-transition model about changes in the Brazilian Cerrado vegetation under influences of fire, wood cutting and grazing. Although successful in certain way, these implementations of the state-transition approach do not explain *why* things happen, because there is no representation of the underlying mechanisms that cause changes in the system. Also, these models lack flexibility, as they aim at describing specific systems and answering particular questions and cannot be (easily) changed or combined to others to address more (or less) complex problems.

One of the most important studies on complexity and stability of biological communities was a qualitative analysis of the results produced by differential equation models about interactions between populations (May, 1973). May's intention was to investigate what can be said if only the topological structure of the trophic web is known, i.e., knowing only the signs (-, 0, +) of the interaction between the species and reasoning with changes over time, that is, with the derivatives of the quantities.

May showed that the 'common-sense wisdom' that more complexity means increased stability may not be true. In his simulations, a less complex community met the conditions for stability, while the more complex was not stable. He points out that this can be a useful approach for modelling quite complex food webs and to capture the general tendencies of the system, bypassing long and complicated steps required by numerical models. However, larger populations violate some of the cri-

teria required for stability analysis and, in these cases, the signs of the interactions alone are not enough, and the interaction magnitudes should be taken into account. This work was inspiring for us, as May reasons with derivatives to draw useful conclusions. Our representation of derivatives does the same job, and qualitative values of quantity magnitudes overcome some of the limitations he mentions. Although we are not able to provide precise answers, qualitative models do not depend on good quality data and fine tuned parameters and provide causal explanations for the system behaviour.

Guerrin and Dumas (2001a,b) describe a model representing empirical knowledge of freshwater ecologists on the functioning of salmon spawning areas. Their model is based on (single) population dynamics and explore mortality at early stages, aiming at predicting and explaining the survival rate of fish under various scenarios. Their approach represents processes that occur at different time-scales (fast and slow) and introduces a real time dating and duration in a purely qualitative model. This model was built according to the so-called constraint-based approach to qualitative reasoning (Kuipers, 1994), which provides qualitative representations of differential equations. Accordingly, knowledge is encoded as constraints and there is no explicit representation of causality. This approach also does not explore the possibility of combining partial model fragments, so it is not possible to reuse models and, doing that, to address more complex problems. Finally, our approach allows for easily implementing and changing assumptions that may reduce the complexity of the simulations, a serious problem for the constraint-based approach.

8. Discussion and concluding remarks

This paper describes an effort to build qualitative models about the complex interactions between four populations in

the ants' garden. Current understanding of the ants' garden is that ants (*Formicidae*), cultivated fungi (*Lepiota*) and bacteria (*Streptomyces*) established a highly interdependent interaction long time ago, in which the bacteria is transmitted from parent to offspring colonies of ants and the fungus is carried by the queens in their mouth when new ant colonies are founded. Ants provide the fungi with a safe environment and raw material (leaves and organic material). *Lepiota* fungi digest the organic matter and provides (becomes) food for the ants that eat the garden. Another group of fungi (*Escovopsis*) was found in colonies and may produce high morbidity and mortality on cultivated fungus. Normally, they do not overgrow the garden because *Streptomyces* produce antibiotics that suppress *Escovopsis* growth. It is also possible that these bacteria produce growth factors used by the cultivated fungi.

Mathematical models about population dynamics, usually built as differential and difference equations, may not be useful to model this problem. Besides the well known difficulties to obtain numerical data of good quality for implementing, calibrating and evaluating these models, it has been shown that such models and their results are difficult to understand and can hardly explain why the systems exhibit certain behaviours.

Qualitative reasoning techniques may be useful to address complex systems like the ants' garden, as they provide means to build comprehensive conceptual models using incomplete knowledge. Qualitative models are not sensitive to arbitrary parameters and allow for valid predictions in situations that mathematical models cannot be used. Some features that may be interesting include the possibility of developing conceptual models with a rich vocabulary to describe objects, quantities, relations, situations, mechanisms of change and conditions for processes to start and finish. Moreover, explicitly represented causality is useful to improve understanding of the structure of ecological systems and to support explanations about the systems behaviour.

Our models of the ants' garden reflect the current understanding of how populations interact ("the consequences of what we believe is true", in Grimm's (1994) words). When information was not available, we assumed the interactions to be as simple as possible. It happens with the interpretation of the relationship between ants and bacteria (commensalisms), bacteria and parasitic fungi (amensalism) and between bacteria and cultivated fungi (commensalisms). Explicitly represented modelling assumptions may either provide alternative perspectives for approaching the system or reduce ambiguity and the number of states in the behaviour graph. These assumptions may easily be changed, and alternative hypotheses can be tested. Using an incremental approach to scale up the complexity of the systems being represented, we developed alternative initial scenarios involving the four populations to fully explore different aspects of the ants' garden system.

The three simulations presented in this paper are relatively small and, therefore, easy to be inspected. Most of the results obtained in these simulations were described by Currie and her co-authors. Contamination of ants' garden by non-mutualistic fungi was found in 39.7% of the samples studied by Currie et al. (1999b), being *Escovopsis* the most abundant.

Thus, the situation described in the initial scenario in simulation 1 is quite common, and the results obtained with the simulation are plausible.

Coexistence of the four populations was observed in more than 70% of the bioassays carried out by (Currie et al., 1999a), and complete elimination of the parasitic fungi was observed in 25% of their bioassays. These results were obtained in simulations 2 and 3, with stabilization of coexisting populations of different sizes and extinction of the parasitic fungi population.

However, some aspects of the ants' garden were not captured by our current version of the models. Bacteria were present in all the colonies of attine ants studied by Currie et al. (1999a). Therefore, the results obtained in states 13 and 14 of simulation 2, in which the population of bacteria was eliminated, were not reported by these authors. Given that no specific knowledge about this restriction was encoded in the models, our results are correct.

Also, according to Currie et al. (1999b), in the absence of ants and sometimes even in their presence, the parasitic fungi may outgrow the cultivated fungi and destroy the garden. This kind of behaviour does not appear in the simulations due to the implemented assumption that both magnitudes and derivatives of *Supply* (the effect of the host on the parasite population) are greater than or equal to, respectively, the magnitudes and derivatives of the quantity *Consumption* (the effect of the parasite on the host population). This assumption, as mentioned in Section 5, keeps the population size of parasites at most equal to the size of hosts. Relaxing this assumption will produce states that show the extinction of the tripartite association of ants, cultivated fungi and bacteria. Finally, Currie and collaborators do not mention any situation in which the whole system disappears. However, it is plausible that this situation happens in the real world.

Ongoing work includes implementations of alternative hypotheses to answer some open questions. For example, the interactions between ants and bacteria, and between bacteria and cultivated fungi may be symbiosis. The idea is to try alternative models in order to make predictions that can be tested; to provide explanations for behaviours observed in the field; and to include new knowledge about the garden. If possible, these qualitative models could be associated with mathematical models, providing a conceptual framework for building the equations. Numerical data could then be used to assess the predictions supported by qualitative models. Exercises of these types may help us to better understand the functioning of complex systems such as the ants' garden.

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