

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 qualitative models 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 an implemented qualitative theory of population dynamics and re-use models about symbiosis, comensalism, amensalism and parasitism. Simulations show the effects of changes in any of the populations on the whole *ants' 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.

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 create a system that can successfully survive in a number of different environments, being the dominant herbivores in the Neotropics. Recent studies [2,3] show 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 happens because ants carry on their body colonies of bacteria (genus *Streptomyces*) that produce antibiotics

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specifically targeted to suppress 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 idea of the ant's garden is shown in Figure 1.

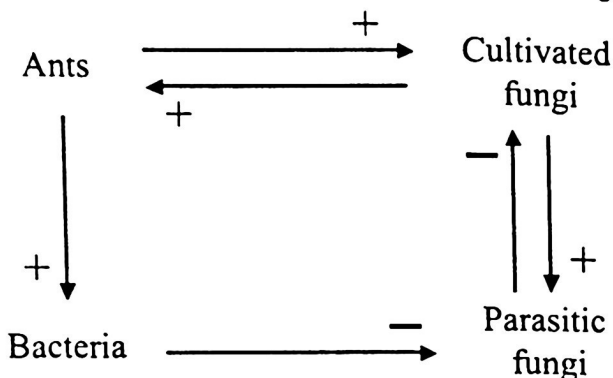


Fig. 1. The ant's garden: positive and negative interactions

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 no clear representation of the system's structure and cannot explain how the system works [7].

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 [14, 15]. For example, modelling interactions among populations with ordinary differential equations, Gilpin [8] 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. [14, 16]).

Qualitative Reasoning (QR) models may play an important role in this discussion. We here describe models about the ants' garden developed from implemented models about single population dynamics, community succession [23], and interactions between two populations [24]. 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's behaviour.

We start presenting the ants' garden problem (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 a full simulation with one of the 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 complete current techniques used in ecological modelling (Section 8).

2 The Problem

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.* [3] noted that these fungi are only known from attine gardens and that they are found in most attine nests. In the absence of ants, rapidly and almost invariably *Escovopsis* overgrow the garden. Instead of multiple contaminants, after removal of tending ants, gardens with 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 [3].

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.* [2] demonstrate that they produce antibiotics that specifically suppress the growth of *Escovopsis*. Further studies indicate that *Streptomyces* produce metabolites (vitamins, aminoacids) that may enhance the growth of the cultivated fungi Currie *et al.* [2].

3 Modelling Approaches to Multispecies 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 a mathematical approach both to field and to experimental population ecology that still is the reference for modelling population dynamics and interactions between populations [12]. Although powerful and elegant, equations pose a number of constraints on the way knowledge is represented, and require good quality data. Because data about ecological systems are often difficult to obtain, available knowledge is incomplete, qualitatively expressed, or just does not exist. To build mathematical models in these conditions is not an easy task. Even though, most of the ecological modelling approaches are based on mathematical equations.

In spite of the wide acceptance of mathematical population ecology [15], during the 1970's 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 nonlinear 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" [15].

A number of experiments were designed to test if non-linearities in natural population dynamics would be enough to produce chaos. The models used were dismissed as simplistic because in general the dynamics of one species involved in a community was seen as if it was alone, although it is known that interactions may restrict one population's behaviour. Whether or not natural populations present chaotic behaviour still is an open question [9].

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 [13] did not support this idea and fired a discussion about whether or not complexity and stability are in fact coupled in biological communities.

Alternative approaches and conceptual models are urgently required to enhance understanding about complex ecological systems. Qualitative Reasoning (QR) models can be an interesting option in a situation like that, providing representations of relevant concepts when mathematical approaches in general are not good options and, even when they are, lack of numerical data hamper their application.

4 QR and Population Ecology Models

We adopted the process oriented ontology [6] and, accordingly, we assume that *processes* are the only mechanism that may cause changes in the system. Two modelling primitives are used to represent the effects of processes: *influences* and *qualitative proportionalities* [6]. Every process is associated to a *rate* and this quantity has a *direct* effect on another quantity (state variable). Changes in directly influenced quantities may propagate to other quantities via qualitative proportionalities. For example, in a tree population the process natality occurs at a rate (birth rate) that should be added to the quantity that represents the population size. This increment on the state variable causes an increase on another quantity, the shaded area covered by the trees. Note that both *influences* and *qualitative proportionalities* associate this causal meaning to a mathematical *rationale*. Direct influences represent the derivative (dX/dt) of the quantity and cause change in the state variable (X). Proportionalities represent monotonic functions involving the quantities, so that when one of them is increasing or decreasing it causes changes on the other quantity (that may also increase or decrease) [6].

The models presented in this paper are implemented using the qualitative simulator GARP [1], which provides adequate representations for the process-oriented ontology, like direct influences ($I+$ and $I-$) and proportionalities ($P+$ and $P-$). Any quantity value in a GARP model is characterized by the tuple $\langle \text{magnitude}, \text{derivative} \rangle$ and the values magnitudes and derivatives may assume are represented in ordered sets, their *Quantity Spaces* (QS). State variables representing the population size 'Number_of' (*Nof*) and the effects each population causes on the other populations use in this implementation of the ants' garden QS = {zero, normal, maximum}. Rates such as birth rate (*B*), death rate (*D*), immigration rate (*Im*) and emigration rate (*E*) use QS = {zero, plus} meaning that they are active or inactive. The basic processes are represented as:

$$I+(\text{Nof}, B); I-(\text{Nof}, \text{Im}); I-(\text{Nof}, D) \text{ and } I-(\text{Nof}, E).$$

Such composition of direct influences creates a qualitative expression of the classical differential equation:

$$dNof/dt = (B+Im) - (D+E).$$

We used proportionalities to model the feedback loop involving the state variable (*Nof*) and the rates (birth rate, death rate and emigration rate), capturing the idea that when *Nof* is increasing or decreasing, the rate is changing in the same direction. For example: $P+(B, Nof)$. This relation does not apply to the immigration process because the size of the population seldom influences the number of immigrated individuals. We represented also an aggregated process (*Population growth*) to combine all the basic population processes, and its rate (*growth rate*) uses the QS = {minus, zero, plus}. These values capture situations in which $(B + Im)$ is smaller than, equal to or bigger than $(D + E)$.

Qualitative models have a number of features that support their use to approach complex systems like the ants and their gardens. They express concepts using a large vocabulary, create explicit representations of causality that may support explanations and use a compositional modelling approach [5] so that a library of more or less independent model fragments can be combined to form a number of different running models. Compositionality involves also re-using 'simpler' models to scale up to more complex systems. In the present case models about single populations and interactions between two populations are re-used here to model the ants' garden.

We assume that the system may be represented as a combination of interactions between pairs of populations. This way, models of symbiosis, predation (parasitism), amensalism and comensalism are re-used to describe the interactions between ants, their cultivated fungi, parasitic fungi and bacteria. Given that model fragments implemented in GARP are problem-independent, knowledge about population and community dynamics already encoded was enough to model the ants' garden. The models are detailed in the next section.

5 The Models

The backbone of GARP models is the description of the entities involved in the model and definitions of how they are related. This is achieved by using a subtype (*isa*) hierarchy representation of the entities and a set of labels that specify structural connections between them. Entities may be objects and concepts. For example, when the objects 'population' and 'tree' are associated by means of the relation 'consists_of' (that is, there exists a population of trees), specific knowledge about populational parameters of trees becomes eligible to be included in the model. Concepts are also organized in subtype hierarchies. This way, concepts can be organized in an isa-hierarchy and then be implemented by using model fragments also organized in a subtype hierarchy manner. In the ants' garden models, concepts like population interaction types and certain types of assumptions are represented as entities.

Interactions such as symbiosis are modelled by a general model fragment 'Symbiosis', which has a set of subtype model fragments implementing typical features of the interaction (for example, the interaction is characterized by mutual positive influences) and some assumptions. *Operating assumptions* play an important role in defining a perspective for approaching the system. It is the case, for example, of the 'closed population assumption' (that changes the definition of the growth equation by taking into consideration only natality and mortality). *Simplifying assumptions* do not change the structure of the system but reduce the number of ambiguities and, thus, may be used to reduce the number of states in a simulation. For example, models about each interaction type include a correspondence between the number of individuals in the population and the strength of the effect it causes on the other population.

Interactions are classified as combinations of the signs {+, 0, -} according to the effects they cause on growth, survival or any other populational attribute (positive, neutral or negative respectively) [21]. Table 1 present the relationships between the four species involved in the ants' garden system, described by Currie and her collaborators [2, 3]. In this table, (+) = the population is positively influenced by the other one; (-) = the population is negatively influenced by the other one; (?) no information available; (**) = self interaction.

The interaction refers to the effects of population in the row on the population in the column. For example: the second row reads as Cultivated Fungi have a positive effect (+) on Ants and Parasitic Fungi and unknown influence (?) on Bacteria.

Table 1. Qualitative relations between four species involved in the ants' garden

| | Ants | Cultiv. Fungi | Paras. Fungi | Bacteria |
|---------------|------|---------------|--------------|----------|
| Ants | ** | + | ? | + |
| Cultiv. Fungi | + | ** | + | ? |
| Paras. Fungi | ? | - | ** | ? |
| Bacteria | ? | + | - | ** |

From the literature relevant interactions can be summarized as follows: Ants / Bacteria = (?, +) and Bacteria / Parasitic Fungi = (?, -). We take a conservative approach and assume that the relations are unidirectional, that is, both Ants and Bacteria are unaffected by the interactions. We therefore define as the minimum set of interactions required to model the ants' garden:

- Ants / Cultivated Fungi = symbiosis (+, +);
- Parasitic Fungi / Cultivated Fungi = parasitism (+, -);
- Ants / Bacteria = comensalism (0, +);
- Bacteria / Parasitic Fungi = amensalism (0, -).

We assume that the effect a population can cause on the other one must be represented as a specific quantity (*Effect*) (see also Figure 2). This option allows for modelling situations in which the quantity *Effect* either corresponds or not to the

population size. This way, there are two quantities that represent the effects of population1 on population2 and vice-versa: *Effect1on2* and *Effect2on1* which can be seen as *Benefit* in positive interactions or *Harm* in negative interactions.

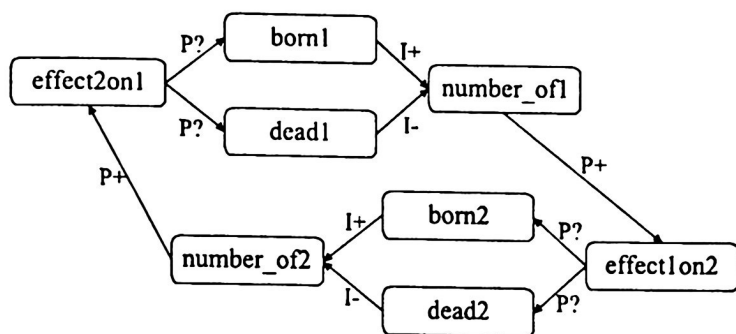


Fig. 2. Two interacting populations [24]

The influences set by the interactions used in the ants' garden model can be summarized as follows:

- (a) Symbiosis: both Effects are positive, reducing D and increasing B;
- (b) Parasitism: the effect of the parasite reduces B2 and increases D2, while effect of the host increases B1 and reduces D2;
- (c) Comensalism: population1 has a positive effect increasing B2 and reducing D2, while population2 does not affect the other one;
- (d) Amensalism: population1 has a negative effect decreasing B2 and increasing D2, while population2 does not affect the other one.

There are some common aspects to all the interactions. First, in this implementation the effects of one population on the other fully correspond to the size of the influencing population. This notion is captured by dependencies between the quantities *Nof* and *Effect*, for example, $P \sim (Effect1on2, Nof1)$.

Second, there is at least one operating assumption associated to each interaction type. These assumptions shape the structure of the system in a particular way. For example, all populations are considered to be *closed* populations (that is, both immigration and emigration rates are equal zero). In the ants' garden models, it is assumed that:

- (a) the quantity spaces of *B* and *D* fully correspond;
- (b) the derivatives of *B* and *D* are equal; and
- (c) the derivative of *Nof* follows the derivative of *D*.

Below we present a summary of the modelling assumptions for each interaction type. Details can be found in Salles et al. [24].

Given that we assume the symbiosis as obligatory for both Ants and Cultivated Fungi, when *Nof1* is zero, as a consequence *Nof2* will be also zero, and vice-versa. In the parasitism between the two species of fungi, it is assumed that the magnitude of *Supply* (the effect of the host on the parasite population) is greater or equal the magnitude of *Consumption* (the effect of the parasite on the host population), and that the derivative of the former is greater or equal than the derivative of the latter. This way, consumption is smaller than or, at most, equal to supply and there is no food shortage.

Four variations of the comensalism between ants and bacteria were implemented:

- (a) if the value of the benefit produced by the ants population is *maximum*, then the bacteria population size also has the value *maximum*;
- (b) if the value of the benefit is *normal*, then the affected population size cannot have the value *maximum*;
- (c) we called 'comensalism high impact' the situation in which the impact of the influencing population is so strong that fully determines changes in the affected population. It was modelled by a relation between the derivatives of the quantities: *d_equal*(Benefit, *Nof2*); and
- (d) the so called 'comensalism medium impact' states that the impact of the benefit partially determines the behaviour of the other population: *d_greater_or_equal*(Benefit, *Nof2*).

Three versions of the amensalism between bacteria and parasitic fungi were implemented, according to the impact caused by the antibiotics:

- (a) if the quantity of antibiotics is maximum, then the other population disappear (*magnitude1*);
- (b) if antibiotics has value normal, then the affected population size has to be smaller than maximum (*magnitude2*); and
- (c) if there is no antibiotics being produced, the other population may assume any value (*magnitude3*). ,

During this modelling effort, we took an incremental approach to experiment with a number of alternative combinations of involving different types of comensalism and amensalism were tested, and different combinations between these assumptions allowed for a broad set of simulation models. Dependencies in the model described in this paper are presented in Figure 3.

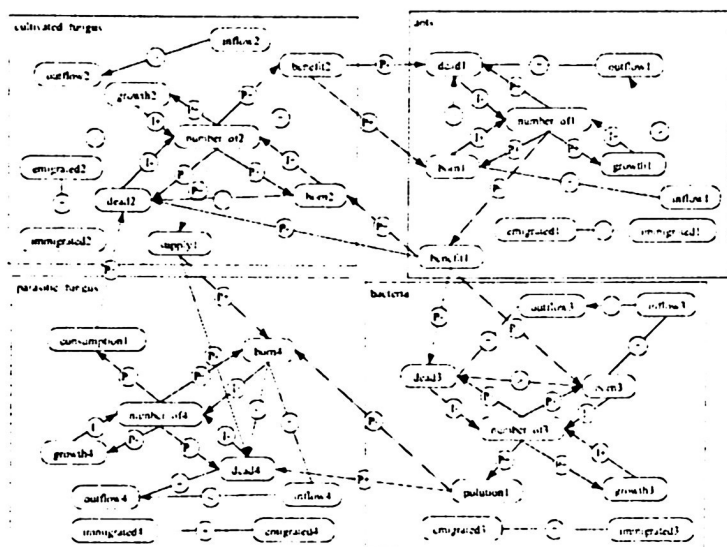


Fig. 3. Causal model of the ants' garden

6 The Simulations

The models support a rich set of simulations, depending on the initial scenarios of the quantities and what assumptions are to be considered. Here we describe a simulation in which the initial scenario adopted the comensalism 'high impact' and the amensalism 'magnitude2' assumptions. The initial values of the state variables were $\langle \text{normal}, ? \rangle$. Figure 4 shows the state-graph generated by the simulation.

This simulation results in 23 states, from which five are end-states (that is, states that do not produce any follow up): [4, 6, 20, 23, 11]. Figure 5 (a-d) shows some behaviour paths of interest to reach these end-states:

- different ways of coexistence,
- complete extinction of the garden,
- Ants and Cultivated Fungi reaching their maximum size,
- and the elimination of the Parasitic Fungi.

The initial scenario produces one state (4) in which all the populations are stable and have values $\langle \text{normal}, \text{zero} \rangle$. This state represents the equilibrium of the system and the coexistence of all the species (Figure 5 (a)). The behaviour path $[5 \rightarrow 7 \rightarrow 6]$ predicts the collapse of the ants' garden, with all the populations going extinct (Figure 5 (b)). Both Ants and Cultivated Fungi go to their maximum size, while bacteria and

Parasitic Fungi are kept with normal values in the behaviour path [2 → 19 → 20] (Figure 5 (c)). Finally, the state-graph shows a behaviour path. [3 → 8 → 11], in which the Parasitic Fungi are eliminated (Figure 5 (d)).

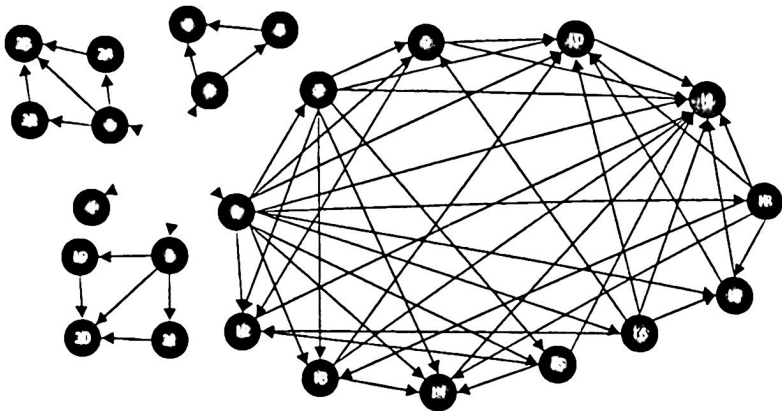


Fig. 4. State graph of a simulation about the ants' garden, starting with the quantity Nof of the four populations equal to <normal.??>

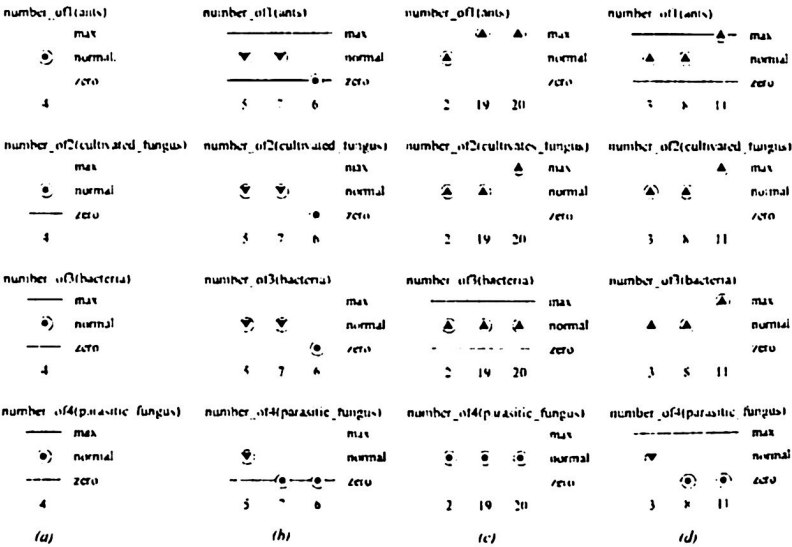


Fig. 5. Selected behaviour paths reaching possible end-states: (a) coexistence and stability; (b) extinction of the four populations; (c) only Ants and Cultivated Fungi reaching their maximum size; (d) Extinction of the Parasitic Fungi

7 Related Work

Given the difficulties of using mathematical models when knowledge is incomplete or numerical data simple does not exist, a number of authors tried alternative approaches for modelling multispecies community dynamics.

Noble & Slatyer [20] and Moore & Noble [18,19] 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.

Guerrin & Dumas [10, 11] describe models representing empirical knowledge of freshwater ecologists on the functioning of salmon spawning areas of salmon and its mortality of 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.

State-transition modelling is often used to describe community dynamics. For example, McIntosh [17] presents a rule-based modelling language to describe succession in communities stressed by fire and grazing using this paradigm. Pivello & Coutinho [22] 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 approaches do not explain *why* things happen, because there is no representation of the underlying mechanisms that cause changes in the system.

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 [13]. May's research question 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. It is pointed 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 criteria 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.

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 (Lepiotaes) and bacteria (Streptomyces) established a highly interdependent interaction long time ago, in which the bacteria is transmitted vertically by ants (that is, from parent to offspring colonies) and the fungus is carried by the queens in their mouth when new ant colonies are founded (that is, horizontally transmitted). Ants provide the fungi with a safe environment and raw material (leaves and organic material). Lepiotaes fungi digest the organic matter and provides (becomes) food for the ants that eat the garden. Another group of fungi (Escovopsis) is often 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 may predict cyclic and chaotic behaviour which we are not sure that apply to natural populations. 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 & Oster[16].

Qualitative Reasoning techniques may be useful to address complex systems like the ants' garden. Some features that may be important include the possibility of developing conceptual models with a rich vocabulary to describe objects, quantities, relations, situations, mechanisms of change, conditions for things start and finish. Also, explicitly represented causality is useful to support explanations about the system behaviour. Moreover, qualitative models may be used to improve understanding of the structure of the ecological system and allow for valid predictions in situations that mathematical models cannot be used.

Our models of the ants' garden reflect the current understanding of how populations interact. 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 (comensalism) and between Bacteria and Parasitic Fungi (amensalism). After explicitly representing modelling assumptions that may either provide alternative perspectives for approaching the system or reduce ambiguity and the number of states in the behaviour graph, the models support a wide range of simulations. Using an incremental approach to scale up the complexity of the systems being represented, we developed alternative initial scenarios involving the four populations. These simulations allow the user to explore a number of possible behaviours. Chaotic behaviour does not appear in coarse-grained models such as those presented here, because quantities do not assume threshold values that would trigger that kind of behaviour.

Ongoing work includes implementations of alternative hypotheses to answer some open questions. For example:

- Bacteria / Cultivated Fungi = (0, +) or (+, +)?
- Ants / Bacteria = (0, +) or (+, +)?
- Bacteria / Parasitic Fungi = (0, -) or (-, -)?

The idea is to try alternative interaction types, in order to predict what should then be observed in the field. Interesting results are coming out from the discussions about which assumptions are required in order to accept that a particular interaction holds between the members of the ants' 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. Some features of qualitative models like the explicit representation of causal dependencies and modelling assumptions, and easy to test alternative hypotheses facilitate the refinement of the model. Exercises of these types may help us to better understand the functioning of complex systems like the ants' garden.

Acknowledgements

We would like to thank Waldenor Barbosa da Cruz for drawing our attention to this beautiful ecological problem and the students enrolled in the course 'Models in Ecology' (2/02) at the University of Brasilia for their enthusiasm and fruitful discussions.

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