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A model for the relationship between the interaction pattern of ecosystems and their fate

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Abstract

The growth of isolated species can be described by simple laws but the fate of ecosystems, where several species interact, is difficult to predict. A crucial point seems to be the identification of regularities in the species interaction patterns that determine the fate of ecosystems. We approach this problem by using an ecosystem of three species whose populations are governed by generalized Lotka–Volterra differential equations. In our model, the species undergo both inter-specific and intra-specific interactions. The inter-specific interactions are positive, null or negative and are parameterized by interaction coefficients ε_{ij} which take values: +1, 0 and −1, respectively. In these conditions, 138 different patterns of interactions (up to species re-labeling) are possible. Two extreme cases for the three intra-specific interactions (self-interactions) are considered: $\varepsilon_{ii} = -1$ and $\varepsilon_{ii} = 0$. We also define *derived parameters*, calculated from the interaction coefficients, which are relevant to determine the survival of species. Comparison of particular patterns shows that the relationship between interaction structure and survival can be subtle and, a priori, unexpected. For instance, we found that adding a negative interaction to a given pattern may be detrimental, indifferent or even beneficial. The same may happen when adding a positive interaction. To make a systematic study of the relationship between structure and fate, first, we perform a "microscopic" study based on the analysis of individual patterns. As a result, we obtained certain general rules or "theorems" concerning the extreme cases of coexistence and extinction of the three species. Second, in order to cover intermediate cases, where precise rules could not be found, we performed "statistical" studies. These provide the probability of survival and coexistence of species as a function of the values of the interaction derived parameters. Among other results, we found that reciprocal cyclic structures, of both positive and negative interactions, and evenly distributed sign balances of input interactions to the species appear to favor survival and coexistence.

Keywords: Coexistence; Ecological models; Indirect effects; Interaction pattern; Population dynamics; Survival

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1. Introduction

Physicists and ecologists approach the investigation of nature from different traditions. The Newtonian tradition of Physics assumes the existence of some few and simple “universal laws” underlying the apparent diversity and complexity of nature. It is mainly predictive and frequently rest on ideal systems (e.g. ideal gas, ideal fluid, etc.). On the other hand, the complexity of most ecological systems has proven to be rather difficult to grasp what has lead ecologists, as biologists of most other fields, to use mainly descriptive approaches and to suspect from caricatures of nature as reliable explanations of reality. This is, perhaps, why ecology lacks from laws similar to the ones of Physics (Harte, 2002).

In recent years, several researchers in the field of theoretical ecology have claimed that contrary to the widespread opinion among ecologists, ecology has general laws similar to those of physics (Murray, 1992; Lawton, 1999; Turchin, 2001). Among the laws proposed is, e.g., the law of exponential growth. It describes the elementary growth behavior of an “isolated” species in “ideal” conditions. However, this law is uninformative about the emergent properties and fate of an ecosystem where the organisms of various species interact. While the growth of isolated species can be described by simple laws, the fate of ecosystems, where several species interact, is difficult to predict. This is because the interplay of simple laws in an intricate network of interactions usually produces unexpected effects. To discover emergent patterns, rules or laws of ecological systems it seems necessary to increase research efforts to introduce in the field new theoretical strategies and frameworks that could tackle the particular complexities of this type of systems. Three necessary ingredients, to achieve this ambitious goal, are the relevant variables, the parameters derived from the interaction coefficients, that could be most adequately related to the variables, and a suitable formal framework that could realize the relationship between them. Size is, of course, another aspect that complicates the study of ecosystems. Therefore, to study the usefulness of the new approaches it is convenient to introduce the complexities step by step, starting with the study of small systems, containing the essence of the problems that we aim to solve. For this reason, in this work we introduce the simplest model that can account for the different possible interactions between two species (competition, mutualism, etc.) in the context of a third species, i.e. a three-species model. The rationale for considering this choice is assessing the way in which the positive or negative actions exerted by one species on another may return to itself not only directly from this species but also indirectly through the third species.

Our aim is to use this toy model to study the repertoire of dynamical behaviors and the kinds of interaction patterns that produce them. More precisely, we are interested in detecting interaction structures that either promote survival and coexistence or doom species to extinction. Concerning the interaction pattern, we will focus on the inter- and intraspecific interactions and several properties derived from them. As we are interested in covering all possible types of interactions between species, we introduce interaction coefficients of three types: positive (those which contribute to population increase), negative (those which contribute to population decrease) and null (those which have no effect on the population numbers). There is, in principle, a myriad of particular functions and parameter values that could quantify the effect of one species on the rate of growth of another. As functional dependence we chose to work with a *generalized Lotka–Volterra* (GLV) model (Goel et al., 1971; Murray, 1993; Pekalski and Stauffer, 1998). Concerning the values of the parameters, we made a series of choices that reduced the huge number of possible combinations to a few representative situations which capture the above-mentioned features that we want to describe.

This work is organized as follows. In Section 2 we describe the model employed. In Section 3, the patterns of interactions are classified according to the value and sign of the interaction coefficients. Several derived structural properties, relevant to our study are defined. In Section 4, we present the overall results of integrating the equations for all the possible patterns of inter-specific interactions, existing in our conditions. We compare individual patterns, showing the subtlety of the relationship between structure and fate. Section 5 is devoted to the analysis of the output presented in the previous section. First, we present a series of simple rules or “theorems” relating interaction pattern and fate that we have obtained for the extreme cases of total extinction and total survival. Many configurations, corresponding to intermediate situations do not