Individual-based model for coevolving competing populations

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Abstract

Classical models for competition between two species usually predict exclusion or divergent evolution of resource exploitation. However, recent experimental data show that coexistence is possible for very similar species competing for the same resources without niche partition. Motivated by this experimental challenge to classical competition theory, we propose an individual-based stochastic competition model, which is essentially a modification of a deterministic Lotka-Volterra type model. The proposed model of competition dynamics incorporates the effects of a discrete genotype, which determines the individual’s adaptation to the environment, as well as its interaction with the other species.

Keywords: Population Dynamics; Lotka-Volterra Model: Competition; Individual-based model.

1 Introduction

Mathematical biology is a fast growing, well recognised area of research. Although not clearly defined yet, is consider one of the most exciting modern
applications of mathematics. The increasing use of mathematics in biology is inevitable as biology becomes more quantitative. The complexity of the biological sciences makes interdisciplinary approach essential. In particular, mathematical modelling of the dynamics of populations interactions is a very challenging and important task.

In building a mathematical description of interacting populations, the main goal is to capture the essential features of a complex trophic web with a mathematically tractable model. The result is, usually, a non-linear dynamical system, which may be expressed as a set of either differential or difference equations. Classical examples are the pioneering works of Lotka (1932) and Volterra (1931). Such models may be understood as describing the time evolution of population averages in a closed ecosystem. In this context, one can devise two broad categories of models: ad hoc models, intended to give a phenomenological mathematical description of the dynamics, and ab initio models, which try to establish sets of dynamical rules based on or inspired by the biology of the populations. The majority of classical population models are deterministic. Recently, due to the growing availability of affordable computer power, individual-based models have been becoming popular. Instead of describing only population sizes, they treat them as collections of individuals with distinctive characteristics. Some of these models have been successful in tackling important biological problems, such as ageing and the evolution of sex (Penna, 1995) and (Oliveira, 1999). The possibility of combining elements of population dynamics and genetics into mathematical models is indeed exciting and promising. Individual-based models are, in general, stochastic models, known to have a rich variety of behaviors, and sometimes differing markedly from their deterministic counterparts.

Classical models for competition between two species usually predict exclusion or divergent evolution of resource exploitation. These predictions are massively corroborated by experience and observation. Such results are commonly summarized in Gause’s competitive exclusion principle: to coexist, species must differ in their resource use; otherwise one of them ends up extinct (Gause, 1935). However, recent experimental data show that coexistence is possible for very similar species competing for the same resources without niche partition (Louzada, 1996).

Motivated by this experimental challenge to classical competition theory, we propose an individual-based stochastic competition model, which is essentially a modification of a deterministic Lotka-Volterra type model. We introduce, as the individual characteristic, a rudimentary “genotype”, which
determines the individual’s adaptation to the environment, as well as its interaction with the other species. In section II we describe the model and its implementation. In section III we present the results of computer simulations of the model proposed in section II, and discuss their implications to coexistence in real ecosystems. We present our final remark and summarize the conclusions in section IV.

2 A model for coevolving competing populations

The continuous-time, deterministic Lotka-Volterra model for competition between two species is given by the equations

$$\frac{dN_i}{dt} = N_i (r_i - \alpha_{ij} N_j) - \alpha_{ii} N_i^2, \quad i, j = 1, 2, \quad j \neq i.$$  \hfill (1)

where $N_i(t), i = 1, 2$ are the populations sizes at time $t$, $r_i, i = 1, 2$ are the intrinsic growth rates; $\alpha_{ij}, i, j = 1, 2$, are the competition strengths.

It is well known that equations (1) have critical points $\vec{N}^{(1)}_{exc} = (r_1/\alpha_{11}, 0)$ and that $\vec{N}^{(2)}_{exc} = (0, r_2/\alpha_{22})$ corresponds to exclusion of one species, while $\vec{N}_{coex} = (r_1 \alpha_{22} - r_2 \alpha_{12}, r_2 \alpha_{11} - r_1 \alpha_{21})/(\alpha_{11} \alpha_{22} - \alpha_{21} \alpha_{12})$ corresponds to coexistence. When $\alpha_{11} \alpha_{22} > \alpha_{12} \alpha_{21}$ the coexistence critical point is globally stable, whereas for $\alpha_{11} \alpha_{22} < \alpha_{12} \alpha_{21}$ the exclusion points are the globally stable ones, and coexistence becomes a saddle point. Put in biological terms, whenever intra-specific competition is stronger than inter-specific competition there can be coexistence; otherwise one species always exclude the other.

We are interested in building a “microscopic” model for competition which is able to mimic the most common biological observations, namely competitive exclusion and coexistence by character displacement. The model should also be able, given some specific conditions, to reproduce the less commonly observed coexistence by converging evolution.

We start by converting equations (1) into probabilistic rules for individual reproduction/death as follows (May, 2001). The intra-specific competition term, $\alpha_{ii} N_i^2$ is interpreted as a death process, giving a death probability $\alpha_{ii} N_i$. The probability that each individual of population $N_i$ reproduces successfully is given by $r_i - \alpha_{ij} N_j, i \neq j$. This simple set of stochastic rules is more easily related to the discretized version of equations (1)

$$N_i(t+1) = N_i(t) + N_i(t) (r_i - \alpha_{ij} N_j(t)) - \alpha_{ii} N_i(t)^2, \quad i, j = 1, 2, \quad j \neq i.$$  \hfill (2)
Now time is a discrete variable, labeling generations, and the parameters should be interpreted as being the ones in equations 1 multiplied by the time interval between generations. It is worth mentioning that the discretized version 2 is identical to the continuous version (equations 1) in the limit of very large populations. Thus, it shares with the continuous model the critical points and their stability properties, as can be easily seen by direct iteration of equation 2.

Up to now the “microscopic” character of the model, meaning its description using rules for individual birth/death processes, can be considered merely formal. It differs from equation 2 only in a well-known demographic stochasticity [6], that is relevant just in the limit of small populations. Our next step is to make the model really “microscopic”, by endowing each individual with a property (which we call a genotype), that will modify competition and intrinsic growth. The phenotype will then be a measure of how close an individual’s genotype is to the optimal genotype for a particular environment. The individual’s genotype is also compared to the genotypes of individuals of the competing species. The closer they are, the stronger the competition is.

Genotypes \( G_i[l] \) are 32-bit strings, associated with individual \( l \) in population \( i \). From each \( G_i[l] \) two phenotypic traits are derived: its normalized Hamming distance to the environmentally determined optimal genotype \( G_{opt} \),

\[
\tau_i[l] = \frac{\langle G_i[l], G_{opt} \rangle}{32},
\]

and its average normalized Hamming distance to the individuals of the opposing population,

\[
\xi_i[l] = \frac{1}{N_j} \sum_{m=1}^{N_j} \frac{\langle G_i[l], G_j[m] \rangle}{32}, \quad j \neq i.
\]

In order to simulate a harsh environment, we impose severe penalties to individuals that depart from \( G_{opt} \): their intrinsic reproduction probability is assumed to decrease exponentially with \( \tau_i[l] \) as

\[
r_i \exp(-\lambda \tau_i[l]),
\]

where \( \lambda \) is a parameter regulating the environment “harshness”. The competition will be modified according to

\[
\alpha_{ij}(1 - \xi_i[l] N_j), \quad j \neq i.
\]
which is a much milder dependence on the phenotype than that imposed by the environment.

In order to allow the species to “evolve”, at every birth event the newborn inherits a copy of its mother’s genotype with a possible “mutation”, represented by a flip of a random bit. The possibility of mutation introduces “real” (as opposed to the formal demographic) stochasticity into the model, and should alter its dynamical behaviour. To investigate the dynamics we simulate the model in a computer.

3 Simulation Results

Our interest is to study the emergence of coexistence other than the “trivial” coexistence of the classical Lotka-Volterra model of equations 1. Thus we start with a situation where intra-specific competition is weaker than inter-specific competition. We also assume, for the time being, symmetric competition ($\alpha_{12} = \alpha_{21}$), and identical initial intrinsic reproduction rates ($r_1 = r_2$). The genotypes of both populations are randomly distributed with uniform probability over the space of 32-bit sequences. No special meaning is attributed to any particular sequence other than the optimal genotype $G_{opt}$.

For the situation just described, the only critical points of the classical model are $\vec{N}_{excl}$. Simulations of the proposed model show evolution towards coexistence, as can be seen in figure 1. There, initial populations are the same, $N_1(0) = N_2(0) = 500$, but the asymptotic steady state is not symmetric. Due to random fluctuations, one of the species is forced to move away from $G_{opt}$, as can be seen in the inset, while the other approaches it as much as possible. This makes the average distance between the two populations genotypes very large, which minimizes the effects of competition. We may interpret this result as the system spontaneously attaining some kind of niche partition.

For $N_1(0) = N_2(0) = 800$ one of the species is excluded. This means that the coexistence state (or states), contrary to the situation in the classical Lotka-Volterra model, has limited basins of attraction, and it is interesting to estimate the sizes of those basins. Starting with $N_1(0) = 1000, N_2(0) = 600$, for example, the system reaches a steady state with average populations different from the case of figure 1. This is an indication of existence of multiple coexistence critical points in this model. Nevertheless, all these coexistence states correspond to niche partition. In figure 2 we plotted the
Figure 1: a) Predator and prey population sizes for initial conditions, and parameters $r_1 = r_2 = 0.8$, $\alpha_{11} = \alpha_{22} = 0.5$, $\alpha_{12} = \alpha_{21} = 0.7$. The black and red curves are populations 1 and 2, respectively, with $N_1(0) = N_2(0) = 500$. b) Average distance between populations’ genotypes and $G_{opt}$, $\bar{\tau}_{av}$, showing evolution towards niche partition. c) First and final distribution of genotypes showing divergent evolution. (The simulation was run for a much longer time than shown to guarantee that the asymptotic regime had been reached).
Figure 2: Sketch of the basin of attraction of the coexistence points (squares) based on simulations with varying initial populations. The squares are initial points from which coexistence is reached.

initial points from which a coexistence state is reached for fixed values of the parameters. As can be seen, the basin of attraction of the stability region is rather limited, in contrast with the classical Lotka-Volterra coexistence point being globally stable.

The simulations also showed cases of coexistence with converging evolution to a single phenotype, corresponding to a distance between individual’s genotypes and $G_{opt}$, that allows for near-maximum variability inside populations. In these cases, exemplified by the results of figure 3, asymptotic inter-specific competition is weaker than the asymptotic intra-specific competition. Once again, evolution leads to a situation compatible with the classical Lotka-Volterra dynamics.

Another interesting case of coexistence has very similar steady-state population sizes and also similar values of $\langle \tau \rangle$, as seen in figure 4. However, the average genotypic distance between populations may be high. This is indeed what happens in this particular case, as can be seen in Fig. 4b. Once again, the system found its way through evolving towards minimal competition, and coexistence is thus possible.
Figure 3: Coexistence with converging evolution. The asymptotic intra-specific competition is larger than the inter-specific competition. a) Population sizes; b) $\tau_{av}$. c) First and final distribution of genotypes showing convergent evolution. (The simulation was run for a much longer time than shown to guarantee that the asymptotic regime had been reached).
Figure 4: Coexistence with converging evolution. a) Population sizes are very similar; b) notice that the average distances $\tau_{av}$, are both large. This is compatible with large initial variability inside each population, what allows for a large average distance between populations' genotypes (blue curve).

4 Concluding remarks

4.1 Qualitative comparison to experiments

The results provided by the proposed model show coexistence attained through minimization of competition. This is compatible with the expectations based on classical population models. However, the observations that motivated this work are not exactly contemplated by our results.

The two species of Dichotomius studied by Louzada et al. show identical patterns of utilization of and preference for resources. Besides, they show identical abundance in all experiments performed to date. Hence, resource sharing can not explain the coexistence of the two species. The fact that the two species exploit identically the temporal, spatial and feeding axes of their niche support the need for a more elaborate explanation of coexistence in Scharabaeidae communities. It may be thought that the mechanism through which these communities minimize competition is related to a sudden change of competitive behaviour: there seems to be a similarity threshold beyond which individuals of different species start to identify each other as pertaining
to the same species, and their competition turns from the inter-specific to
the intra-specific type. This mechanism is completely absent from the model
proposed in this work. We are investigating possible modifications of the
proposed model to take this kind of mechanism into account.

4.2 Summary of results

We presented an individual-based model for the dynamics of two coevolving
competing species. It is an extension of the Lotka-Volterra equations for com-
petition to include coevolution. The dynamical behaviour of the proposed
model shows important differences from the classical Lotka-Volterra com-
petition, such as multiple coexistence critical points with limited attraction
basins. The coevolution dynamics mimics important biological behaviours
such as niche partition and converging evolution. Modifications of the present
model to reproduce other kinds of experimentally observed behaviour are un-
derway.

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