Evolutionary dynamics and competition stabilize three-species predator–prey communities

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ABSTRACT

We perform individual-based Monte Carlo simulations in a community consisting of two predator species that compete for a single prey species, with the purpose of studying biodiversity stabilization in this simple model system. Predators are characterized with predation efficiency and death rates, to which evolutionary adaptation is introduced. Competition for limited prey abundance drives the populations' optimization with respect to predation efficiency and death rates. We study the influence of various ecological elements on the final state, finding that both indirect competition and evolutionary adaptation are insufficient to yield a stable ecosystem. However, (quasi-stable) three-species coexistence is observed when direct interaction between the two predator species is implemented.

1. Introduction

Ever since Darwin first introduced his theory that interspecific competition positively contributes to ecological character displacement and adaptive divergence (Darwin, 1859), debates have abounded about its importance in biodiversity. Character displacement is considered to occur when a phenotypical feature of an organism, which could be morphological, ecological, behavioral, or physiological (for example, beak size) (Brown and Wilson, 1956), is shifted in a statistically significant manner due to the introduction of a competitor (Schluter and McPhail, 1992; Taper and Case, 1992). One example of ecological character displacement is that the body size of an island lizard species becomes reduced on average upon the arrival of a second, competing lizard kind (Melville, 2002). Early observational and experimental studies of wild animals provided support for Darwinian evolutionary theory (Brown and Wilson, 1956; Lack, 1947). One famous observation related to finches, whose beak size would change in generations because of competition (Lack, 1947). However, recent studies using modern genetic analysis techniques do not find genome modifications to the same extent as phenotypic beak changes, thereby casting doubt on Darwin's observational studies (Arthur, 1982; Grant, 1975). Another concern with experiments on birds or other animal species is that they may live for decades, rendering this sort of study too time-consuming. Evolutionary theory is based on the assumption that interspecific competition occurs mostly between closely related species because they share similar food resources, thus characters exploiting new resources

are preferred. Ecologists perform experiments with wild animals by introducing a second competing species and recording their observable characters such as, e.g., body size, beak length, and others (Arthur, 1982; Melville, 2002). Unfortunately, direct control over natural ecosystems is usually quite limited; for example, ecological character displacement with wild animals cannot be shut down at will in natural habitats. However, this is easily doable in carefully designed computer simulations.

Game theory has a long history in the study of biological problems (Smith, 1982). Among all the mathematical models of studying biodiversity in ecology, the Lotka–Volterra (LV) (Lotka, 1920; Volterra, 1926) predator–prey model may rank as possibly the simplest one. Only one predator and one prey species are assumed to exist in the system. Individuals from each species are regarded as simple particles with their reaction rates set uniformly and spatially homogeneous. They display three kinds of behaviors which are influenced by pre-determined reaction rates: prey particles may reproduce, predator particles can spontaneously die, and predators may remove a prey particle and simultaneously reproduce. This simple LV model kinetics may straightforwardly be implemented on a regular lattice (usually square in two or cubic in three dimensions) to simulate situations in nature, where stochasticity as well as spatio-temporal correlations play an important role (Antal and Droz, 2001; Boccara et al., 1994; Chen and Täuber, 2016; Droz and Pękalski, 2001; Durrett, 1999; Kowalik et al., 2002; Lipowski, 1999; Lipowski and Lipowska, 2000; Matsuda et al., 1992; Mobilia et al., 2006a,b; Monetti et al., 2000; Provata et al., 1999; Rozenfeld and

Albano, 1999; Satulovsky and Tomé, 1994; Washenberger et al., 2007). It is observed in such spatial stochastic LV model systems that predator and prey species may coexist in a quasi-stable steady state where both populations reach non-zero densities that remain constant in time; here, the population density is defined as the particle number of one species divided by the total number of lattice sites. Mapping the fundamental master equation for the stochastic LV model to a continuum field theory action allows a systematic perturbation expansion analysis for the fluctuation- and correlation-induced renormalizations of system parameters (Täuber, 2012). We also note that a recent study applies spatial moment equations to predator–prey dynamics to go beyond simple mass-action dynamics (Barraquand and Murrell, 2013). Considering that the original LV model contains only two species, we here aim to modify it to study a multi-species system. We remark that there are other, distinct well-studied three-species models, including the rock-paper-scissors model (Dobramysl et al., 2018; Frachebourg et al., 1996), which is designed to study cyclic competitions, a food-chain-like three-species model (Shih and Goldenfeld, 2014), as well as more general networks of competing species (Dobramysl et al., 2018) and food webs (Allhoff et al., 2015; Drossel et al., 2001; Rossberg et al., 2008), all of which contain species that operate both as a predator and a prey. In this paper we mainly focus on predator–prey competitions, where any given species plays only one of those ecological roles.

The outcome of games involving two or more predator species competing for the same resource or prey has been discussed in the seminal work by Gause and developed into his competitive exclusion principle (Gause, 1934), which was later framed in the context of ecological niches (Slobodkin, 1961). Levin extended these results, finding that N distinct species cannot coexist stably as long as there are less than N limiting factors (Levin, 1970). This principle has undergone some qualification over time: It has been shown that spatially heterogeneous habitat structure (Hanski, 1981) may lead to stable coexistence or that stable coexistence of two parasites of the same host is possible, albeit only when direct parasite competition is included and if the hosts are allowed to recover from infection (Hochberg and Holt, 1990).

Compared with the original LV model, we introduce one more predator into the system so that there are two predator species competing for the same prey. We find that even in a spatially extended and stochastic setting, the 'weaker' of the two predator species will die out fast if all reaction rates are fixed. Afterwards the remaining two species form a standard LV system and approach stable steady-state densities. Next we further modify the model by introducing evolutionary adaptation (Dobramysl and Täuber, 2013a). We also add a positive lower bound to the predator death rates in order to avoid 'immortal' individuals. Finally, we incorporate additional direct competition between predator particles. (Quasi-)stable multiple-species coexistence states are then observed in certain parameter regions, demonstrating that adaptive evolution in combination with direct competition between the predator species facilitates ecosystem stability. Our work thus yields insight into the interplay between evolutionary processes and inter-species competition and their respective roles to establish and maintain biodiversity.
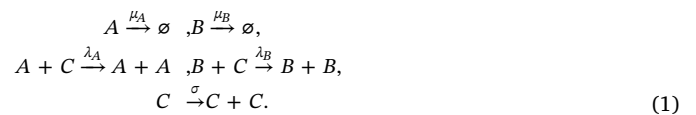
2. Stochastic lattice Lotka–Volterra model with fixed reaction rates

2.1. Model description

We spatially extend the LV model by implementing it on a two-dimensional square lattice with an edge length of $L = 512$ lattice sites. It is assumed that there are three species in the system: two predator species A, B, and a single prey species C. Our model ignores the detailed features and characters of real organisms, and instead uses simple 'particles' to represent the individuals of each species. These particles are all located on lattice sites in a two-dimensional space with periodic boundary conditions (i.e., on a torus) to minimize boundary effects. Site

exclusion is imposed to simulate the natural situation that the local population carrying capacity is finite: Each lattice site can hold at most one particle, i.e., is either occupied by one 'predator' A or B, occupied by one 'prey' C, or remains empty. This simple model partly captures the population dynamics of a real ecological system because the particles can predate, reproduce, and spontaneously die out; these processes represent the three main reactions directly affecting population number changes. There is no specific hopping process during the simulation so that a particle will never spontaneously migrate to other sites. However, effective diffusion is brought in by locating the offspring particles on neighboring sites of the parent particles in the reproduction process (Chen and Täuber, 2016; Mobilia et al., 2006b). Adding nearest-neighbor migration would thus not markedly change the simulation outcome provided this additional hopping rate is not drastically higher than all the other reaction rates. For high diffusivities, spatial fluctuations become suppressed, and the system is essentially described by the mean-field reaction-diffusion equations for local population densities (Täuber, 2012).

The stochastic reactions between neighboring particles are described as follows:

$$A \xrightarrow{\mu_A} \varnothing \quad , B \xrightarrow{\mu_B} \varnothing,$$
$$A + C \xrightarrow{\lambda_A} A + A \quad , B + C \xrightarrow{\lambda_B} B + B,$$
$$C \xrightarrow{\sigma} C + C. \tag{1}$$

A 'predator' A (or B) may spontaneously die with decay rate μ_A (μ_B) > 0. Predators may consume a neighboring prey particle C, and simultaneously reproduce with 'predation' rate λ_A (λ_B), which is to replace C with a new predator particle in the simulation. In nature, predation and predator offspring production are separate processes. But such an explicit separation would not introduce qualitative differences in a stochastic spatially extended system in dimensions $d < 4$ (Mobilia et al., 2006a). When a prey particle has an empty neighboring site, it can generate a new offspring prey individual there with birth rate $\sigma > 0$. Note that a separate prey death process $C \rightarrow 0$ can be trivially described by lowering the prey reproduction rate and is therefore not included. We assume asexual reproduction for all three species, i.e., only one parent particle is involved in the reproduction process. Each species consists of homogeneous particles with identical reaction rates. Predator species A and B may be considered as close relatives since they display similar behavior (decay, predation and reproduction, effective diffusion) and most importantly share the same mobile food source C. For now, we do not include evolution in the reproduction processes, therefore all offspring particles are exact clones of their parents. We are now going to show that these two related predator species can never coexist.

2.2. Mean-field rate equations

The mean-field approximation ignores spatial and temporal correlations and fluctuations, and instead assumes the system to be spatially well-mixed. We define $a(t)$ and $b(t)$ as the predators' population densities and $c(t)$ as the prey density. Each predator population decreases with death rate $\hat{\mu}$ (exponential population decay), but increases with the predation rate $\hat{\lambda}$ and prey density $c(t)$ (LV predation). The prey population $c(t)$ increases exponentially with its reproduction rate $\hat{\sigma}$ which is checked by a finite carrying capacity (logistic growth law), and decreases with growing predator population densities. The mean-field rate equations consequently read

$$\frac{da(t)}{dt} = -\hat{\mu}_A a(t) + \varepsilon\hat{\lambda}_A a(t) c(t),$$
$$\frac{db(t)}{dt} = -\hat{\mu}_B b(t) + \varepsilon\hat{\lambda}_B b(t) c(t),$$
$$\frac{dc(t)}{dt} = \hat{\sigma} c(t)\left[1 - \frac{a(t) + b(t) + c(t)}{K}\right] - \hat{\lambda}_A a(t) c(t) - \hat{\lambda}_B b(t) c(t). \tag{2}$$