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Coexistence and superior competitor exclusion in the Leslie–Gower competition model with fast dispersal

Marcos Marvá*, Rafael Bravo de la Parra

Departamento de Física y Matemáticas, Universidad de Alcalá, Alcalá de Henares, Spain

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ABSTRACT

In this work, we study a nonlinear two time scales discrete competition model. Specifically, we deal with a spatially distributed Leslie–Gower competition model with fast dispersal. After building up the corresponding two time scales model, we have used approximate aggregation techniques to derive a lower dimensional, reduced system. When the ratio between time scales is large enough, the aggregated system can be used to analyze the two time scales model.

As a result, we have found trade-off mechanisms between fast dispersal and competition under spatial homogeneity conditions. When the environment is heterogeneous, we have found that under asymmetric dispersal, whether competitive coexistence or competitive exclusion occurs depends on the initial population sizes of the two species.

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1. Introduction

The analysis of the mechanisms underlying coexistence in patchy environments is an important issue in theoretical ecology (Levins, 1969, 1970; Levin, 1992). Essentially, species competition and individuals dispersal are taken into account and the interest relies on the interplay between both processes.

One of its paradigms, the Patch Occupancy Metapopulation Theory (POT) (Hanski, 1999), explores population persistence and species coexistence in patchy landscapes using the competition-colonization trade-off as its basis. The POT focuses on the presence of local populations in habitat patches and it does not include any description of local dynamics. The POT implicitly recognizes that competition operates at a much faster time scale than colonization-extinction processes. All these assumptions preclude, in fact, local coexistence and imply that migration cannot influence local competitive interactions. The POT and its predictions are, nevertheless, at odds with some empirical data (Lei and Hanski, 1998) due to the implicit separation of time scales.

In Amarasekare and Nisbet (2001) it is set up a metapopulation model considering dispersal and competition within the same time scale. Under this assumption, the authors shown that in a spatially homogeneous competitive environment differences in species dispersal are not enough to explain coexistence with the absence of a refuge for the weaker competitor. Besides, they considered spatial heterogeneity either by allowing for species refuges or by assuming variations in competitive rankings over space such that the superior competitor in some parts of the landscape becomes the inferior competitor in the remnant landscape. The heterogeneity is concreted in spatial variance in fitness that leads to a source-sink dynamics framework enabling coexistence.

Finally, the puzzle was completed in Nguyen Ngoc et al. (2010) where dispersal was assumed to be much faster that competition. Under these settings, the authors shown that there is a trade-off between fast dispersal and competition when the environment is homogeneous. In particular, appropriate dispersal rates may allow the weaker competitor to survive and even to exclude the stronger competitor.

The approaches presented in Hanski (1999) and Nguyen Ngoc et al. (2010) share the feature that competition and dispersion occur at different time scales. Understanding how ecological phenomena interact across temporal scales is crucial in theoretical ecology (Levin, 1992; Leibold et al., 2004), since it is known that differences in process time scales may be critical for system dynamical behaviour (Ludwig et al., 1978; Leibold et al., 2004; Lett et al., 2005).

The aim of this work is to analyze the interplay of species competition and fast individuals dispersal in a metapopulation, in the sense that we seek trade-off mechanism between these two processes related to species coexistence. We also study the role of spatial heterogeneity in the aforementioned compensation mechanism. Here, we focus on the impact of dispersal on local populations

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* Corresponding author. Tel.: +34 918854900
E-mail addresses: marcos.marva@uah.es (M. Marvá), rafael.bravo@uah.es (R.B. de la Parra).

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with discrete non-overlapping generations. This situation can be found in a range of evolutionary and ecological processes in which gene flow and dispersal rate due to non sedentary habits can operate at a fast scale relative to selection or population interaction processes (Nguyen Ngoc et al., 2010). The corresponding mathematical models adopt the form of systems of difference equations (Yakubu and Castillo-Chávez, 2002). The study of the role of dispersal in continuous-time metapopulation models is extensive (Levin, 1992; Amarasekare, 2003; Bowne and Bowers, 2004; Nguyen Ngoc et al., 2010).

The paradigms of competition models are the Lotka–Volterra model in the continuous case and the Leslie–Gower model (Leslie and Gower, 1958) in the discrete case. The latter played a fundamental role in laboratory experiments with the flour beetle (of the genus *Tribolium*) that give rise to the competitive exclusion principle that is one of the important tenets in ecology (Park, 1948, 1954, 1957; Park et al., 1964; Leslie and Gower, 1958). The Leslie–Gower model consists of two Beverton–Holt equations with the adding of the interspecific competition.

The proposed model considers two competing species inhabiting an environment consisting of p different patches. The model couples local Leslie–Gower competition dynamics with linear (constant rates) individuals dispersal between patches. Dispersal is assumed to be faster than competition, which yields a system of $2p$ difference equations with two time scales. Taking advantage of the time scales separation the system can be studied in terms of a two dimensional system for the total densities of the two species. This reduction is performed with the help of the so-called approximate aggregation of variable technique (Auger et al., 2008; Bravo de la Parra et al., 2013). The form of the reduced system is that of a discrete competition model different from the Leslie–Gower model and with a richer dynamics.

The Leslie–Gower model exhibits the same dynamics (Cushing et al., 2004; Liu and Elaydi, 2001) than the Lotka–Volterra model. Weak species competition leads to a coexistence equilibrium state while strong species competition makes competitive exclusion to occur: which species gets extinct either depends on priority effects (the excluded species depend on the initial amount of individuals, the species that gains an early advantage wins) or do not. The laboratory results with the flour beetle where mostly supported by the Leslie–Gower competition model. Nevertheless, data from one of those experiments was at odds with this model, since in this experiment whether competitive coexistence occurred or competitive exclusion occurred depended on the initial population numbers of the two species (Cushing et al., 2004). In Cushing et al. (2004, 2007) an explanation to this data is proposed in terms of an age structured population model by introducing a Ricker-type nonlinearity and found multiple mixed-type attractors. Instead, the model that we propose keeps as local dynamics the simple Leslie–Gower model but we find that together with fast dispersal there exist scenarios displaying multiple equilibrium attractors that compatible with the data observed in the experiments with the flour beetle and are different from those displayed in Cushing et al. (2004, 2007) (see Section 4).

This work is organized as follows: in Section 2 we set up a slow-fast Leslie–Gower spatially distributed competition model. The habitat consists of p patches and there individuals dispersal. The system consists of $2p$ equations and we sketch both a dimension reduction procedure as well as the kind of information that produces. Section 3 is devoted to the analysis of the reduced system. We derive general conditions for species viability, species coexistence or species extinction. Nevertheless, under the most general settings, the model depends on so many parameters to perform a complete analysis. In Section 3.1, we deal with the important case of an a 2 patches environment. In this case we show that fast dispersal in heterogeneous environments may lead to scenarios with two and even three stable equilibrium points (bi-stability and tri-stability), while it is not possible if both patches are homogeneous. Besides, we highlight a trade-off mechanism between dispersal and competition. We discuss the previous results in Sections 4 and 5 contains the conclusions of this work. Appendix A devoted to prove the mathematical results completes the manuscript.

2. Methods

In this section we set up a difference equation (discrete time) model that accounts species competition along with fast dispersal. After building the slow fast model, the separation of time scales allows us to apply the results sketched in Appendix A and get a less dimensional system. The section finishes with a result which describes which kind of information about the slow fast system can be retrieved from the reduced system.

2.1. Presentation of the model

We consider two competing species inhabiting an environment divided into p patches. Let $n_i^j(t)$ be the number of individuals of species $i = 1, 2$ in patch $j = 1, \ldots, p$ at time t. We denote $N_i(t) = (n_i^1(t), n_i^2(t), \ldots, n_i^p(t))$, the spatial distribution of individuals of each species and the population vector

$$N(t) = (N_1(t), N_2(t))^T,$$

where the superscript T stands for transposition. We assume that individual displacements between patches are faster than the local community dynamics. Following Appendix A both processes, dispersal and local dynamics, are represented by two mappings F (for fast) and S (for slow), respectively. The time unit of the system is that of the slow process and the effect of the fast dynamics is represented by the kth iterate of mapping F, $F^{(k)}$, with k being an approximation of the time scales ratio. Thus, we set the so called complete system that combines both processes, fast and slow, and that reads as follows:

$$N(t+1) = S(F^{(k)}(N(t))) \tag{1}$$

Next, we explicitly define the mappings F and S.

We assume that dispersal rates are constant and we denote f_i^{rs} the fraction of individuals of species i moving from patch s to patch r. Gathering these coefficients we define the dispersal matrices $\mathcal{F}_i = (f_i^{rs})$, $i = 1, 2$, that are stochastic. For further purposes, we also assume that they are regular. The definition of mapping F representing dispersal is thus

$$F(N) = \begin{pmatrix} \mathcal{F}_1 & 0 \\ 0 & \mathcal{F}_2 \end{pmatrix} \begin{pmatrix} N_1^T \\ N_2^T \end{pmatrix} = \mathcal{F}N \tag{2}$$

The local species competition in each patch $j = 1, \cdots, p$ is represented by the Leslie–Gower model (Cushing et al., 2004). If n_1^j and n_2^j are the number of individuals of both species in patch j, after a time unit they become, respectively

$$\begin{cases} \dfrac{b_1^j}{1 + c_{11}^j n_1^j + c_{12}^j n_1^j} n_1^j = s_1^j(n_1^j, n_2^j), \\ \dfrac{b_2^j}{1 + c_{21}^j n_2^j + c_{22}^j n_2^j} n_2^j = s_2^j(n_1^j, n_2^j), \end{cases}$$

where b_i^j is the intrinsic growth rate of species i in patch j (that is, the growth rate without taken into account density dependent effects) and c_{rs}^j measures the competitive effect of species s on

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