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Dynamics of a pioneer–climax species model with migration

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ABSTRACT

A pioneer–climax species model with migration is presented. It is shown that the system can present a variety of configurations which represent competitive exclusion scenarios and coexistence scenarios, including coexistence under sustained oscillation scenarios. We analyze all the possible configurations for key dynamical parameters. We study the transitions among configurations due to changes in the dynamical parameters, and discuss the biological relevance of these findings.

1. Introduction

Different types of modeling techniques have been used to model the interactions of competing species whose reproductive capacity is sensitive to the population density in their shared ecosystem (see for instance [1–5]). The dynamics of pioneer–climax species models have been widely studied for the last two decades [6–16]. Buchanan [9] presented models with explicit spatial distribution and diffusion rates, has shown stability of steady states and has provided necessary conditions for the formation of spatial patterns in species densities. Also, Buchanan [9] and Sumner [16] have considered constant stocking and harvesting as a mechanism for reversing bifurcations in forest ecosystems. In this work, we mainly focus on the effects produced by the density-dependent migration from the ecosystem of pioneer–climax species. Such ecosystems are assumed to have two kinds of species interactions: intraspecific and interspecific. We consider linear and quadratic fitness functions, similar in behavior to the ones used by Hassell and Comins [5], and Ricker [17] for the pioneer species, and Selgrade and Namkoong [13] for the climax species. We are interested in identifying the role that the constant dynamical parameters play in the appearance and disappearance of stable steady states, and even periodic or oscillatory solutions. We analyze all possible configurations obtained by varying the critical parameters, and establish explicit conditions for the transitions among them, including two Hopf type bifurcation cases. The global stability of the system has been also completely analyzed. Competitive exclusion scenarios, cases in which one of the species becomes extinct, and coexistence scenarios, including coexistence under oscillations, have been found.

The organization of this paper is as follows. In Section 2, the two species pioneer–climax model system with migration and properties of the fitness functions are described. In Section 3, we study the dynamics of the pioneer–climax species ecosystem with migration, considering linear and quadratic fitness functions. The vector fields and equilibrium points of a total of thirteen possible nullcline configurations are studied. The variation of bifurcation parameters leading to Hopf bifurcations and the appearance of periodic orbits, and the effect of changes in the values for the dynamical parameters of the

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ecosystem, are also studied. Section 4 deals with the biological implications of variations in the values for the migration and intraspecific parameters, and transitions among diverse coexistence and competitive exclusion scenarios.

2. The pioneer–climax model system with migration

The pioneer–climax model of interest describes the dynamics of a two species ecosystem with migration, and it is proposed to be given by the following pair of coupled ordinary differential equations:

$$\frac{dn_1}{dt} = n_1 f_1(z_1) - bn_1, \tag{1}$$

$$\frac{dn_2}{dt} = n_2 f_2(z_2) - dn_2, \tag{2}$$

where n_1 and n_2 represent the population density for the pioneer and climax species, respectively. $f_1(z_1)$ represents the pioneer fitness function, and $f_2(z_2)$ is the climax fitness function. The variables z_i $(i = 1, 2)$ represent weighted population densities given as follows

$$z_1 = c_{11}n_1 + c_{12}n_2, \tag{3}$$

$$z_2 = c_{21}n_1 + c_{22}n_2. \tag{4}$$

The constant parameters $c_{ij} > 0$ $(i, j = 1, 2)$ are called interaction coefficients and describe the intraspecific and interspecific competitive effect. Rescaling z_i through the transformation $z_i \rightarrow z_i/c_{ij}$ $(i \neq j,\, c_{ij} \neq 0)$ allows us to choose $c_{12} = c_{21} = 1$. These values for c_{12} and c_{21} will be considered throughout the paper.

The terms bn_1 and dn_2 in the right-hand side of Eqs. (1) and (2) are subtracted in order to describe the species migration of the system. We will focus on positive values of b and d, although in the model they could also take negative values. b and d represent immigration rates when they are negative, and emigration rates when they are positive.

Even though in this case the migration rates could be factored into the functions f_1 and f_2, it is of interest to know the specific role that they play in larger systems. One main reason for singling out the migration rate is the fact that in a metapopulation case we would like to understand whether such factors are able to stabilize or destabilize, or even cause Hopf bifurcation in any part of the complete system. The specific case we consider is of the form

$$\frac{dn_1}{dt} = n_1 f_1(z_1) - bn_1, \tag{5}$$

$$\frac{dn_2}{dt} = n_2 f_2(z_2) - dn_2, \tag{6}$$

$$\frac{dm_1}{dt} = m_1 f_3(z_3) + bn_1, \tag{7}$$

$$\frac{dm_2}{dt} = m_2 f_4(z_4) + dn_2. \tag{8}$$

where m_1 and m_2 represent the population density for the pioneer and climax species, respectively, inhabiting a proposed immigration patch. Even though the final goal of this investigation is to analyze system (5)–(8), the fact that we allow general functions f_1, f_2, f_3 and f_4 makes its behavior potentially a very complicated one. That is the main reason for starting the study of system (1)–(2), which is also embedded in Eqs. (5) and (6), and in Eqs. (7) and (8). Imagine a system in which each single patch is described either by Eqs. (5) and (6) or by Eqs. (7) and (8), without migration between patches. Assume the behavior of each separated system is well understood. Further, assume that for almost all initial conditions the corresponding solutions tend to a steady state or even a stable periodic solution. If at a certain point in time some environmental changes allow migration between patches, what would be the effect of the absence of the outgoing individuals on the originating patch? How would the newcomer contribute to the dynamics of the complete system? Which of the two effects, emigration or immigration, would out-weight the other? Is it possible that a completely new dynamics sets in? Before answering this questions, we should be able to understand the changes that emigration or immigration produce in each single patch for general functions f_1 and f_2. That is the aim of the present work. The dynamics of the whole ecosystem (5)–(8) will be studied in a later paper. In the subsystem given by Eqs. (7) and (8), $f_3(z_3)$ and $f_4(z_4)$ are again the pioneer and climax fitness functions, respectively. The variables z_i $(i = 3, 4)$ represent weighted population densities similar to those ones for $f_1(z_1)$ and $f_2(z_2)$ given in Eqs. (3) and (4). The last terms in the right-hand side of Eqs. (7) and (8) represent the arrival of species n_1 and n_2 into the proposed immigration patch.

An example of possible functions f_1 is the exponential pioneer fitness function that Ricker [17] concluded for certain fish populations

$$f(y) = e^{a(1-y)}. \tag{9}$$

Also, Hassell and Comins [5] studied pioneer fitness functions given in the following form