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Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation

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ABSTRACT

The standard model for the dynamics of a fragmented density-dependent population is built from several local logistic models coupled by migrations. First introduced in the 1970s and used in innumerable articles, this standard model applied to a two-patch situation has never been completely analysed. Here, we complete this analysis and we delineate the conditions under which fragmentation associated to dispersal is either beneficial or detrimental to total population abundance. Therefore, this is a contribution to the SLOSS question. Importantly, we also show that, depending on the underlying mechanism, there is no unique way to generalize the logistic model to a patchy situation. In many cases, the standard model is not the correct generalization. We analyse several alternative models and compare their predictions. Finally, we emphasize the shortcomings of the logistic model when written in the r-K parameterization and we explain why Verhulst's original polynomial expression is to be preferred.

1. Introduction

The theoretical literature on spatially-distributed population dynamics is huge and we will make no attempt to review it. Instead, we will focus on some problems with the basic models that are used as the building blocks of this body of theory. Indeed, we have found that even the simplest and most ancient model still contained unresolved aspects and that unsupported generalizations were common. More precisely, we will explore the details of various ways to generalize the logistic model to a two-patch situation, i.e., the simplest way to describe the dynamics of a spatially-distributed, density-dependent population. The standard model commonly used in this situation has never been completely analysed. We will complete this analysis and we will delineate the conditions under which fragmentation can either be beneficial or detrimental to total population abundance. More importantly, we will show that this standard multi-patch logistic model is, in many cases, an incorrect description of the dynamics of a fragmented density-dependent population.

Assume that some population N follows the logistic model when growing in a uniform environment:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right). \tag{1}$$

This model assumes perfect mixing of the population. For modelling the dynamics of the same species in a patchy environment, it is widely accepted to assume that each subpopulation in each patch follows a local logistic law and that the various patches are coupled by migrations. Taking the case of two patches as a simple example, the following model describes logistic growth in two patches linked symmetrically by migration:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1\left(1 - \dfrac{N_1}{K_1}\right) + \beta(N_2 - N_1), \\ \dfrac{dN_2}{dt} = r_2 N_2\left(1 - \dfrac{N_2}{K_2}\right) + \beta(N_1 - N_2), \end{cases} \tag{2}$$

where N_i is the population abundance in patch i and βN_i is the emigration flow from patch i to the other patch ($\beta \geq 0$). The

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parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity in patch i. This model was first studied by Freedman and Waltman (1977), later by DeAngelis et al. (1979) and Holt (1985), and a graphical presentation was given by Hanski (1999, pp. 43–46) in his reference book on metapopulations. More recently, DeAngelis and Zhang (2014) have brought new developments.

We denote by N_1^* and N_2^* the population abundances at equilibrium. With no loss of generality, we assume that patch 1 has the lower carrying capacity (i.e., $K_1 \leq K_2$). In isolation ($\beta = 0$), each population equilibrates at its local carrying capacity: $N_i^* = K_i$.

A well-known result is that, in the presence of dispersal ($\beta > 0$), the total equilibrium population, $N_T^* = N_1^* + N_2^*$, is generally different from the sum of the carrying capacities $K_1 + K_2$. Freedman and Waltman (1977) have shown that, in the case of perfect mixing ($\beta \to \infty$), both patch populations tend to equal values and that the total equilibrium population tends to:

$$N_T^* = K_1 + K_2 + (K_1 - K_2)\frac{r_1K_2 - r_2K_1}{r_1K_2 + r_2K_1}, \quad \text{in the limit } \beta \to \infty. \tag{3}$$

(Note that this expression contained typos in Freedman and Waltman, 1977, their equation 3.3 that were only partially corrected by Holt, 1985.)

Depending on the sign of the numerator present in Eq. (3), dispersal can either be beneficial or detrimental with respect to the total carrying capacity. Thus, if $r_1K_2 < r_2K_1$ (with $K_1 < K_2$), we will have

$$N_T^* > K_1 + K_2, \quad \text{if } \beta \text{ is sufficiently large.} \tag{4}$$

This spectacular result, somewhat paradoxical, has been widely discussed and has led to speculations about the general virtues of patchiness and dispersal, for example in the context of the conservation ecology question of whether a single large refuge is better or worse than several small ones (the SLOSS debate; see, e.g., Hanski, 1999).

Freedman and Waltman (1977) only contrasted the situations of perfect isolation and perfect mixing; they did not study the effect of intermediate values of the dispersal parameter β. This effect was studied in the recent paper of DeAngelis and Zhang (2014), but only in the special case $r_1/K_1 = r_2/K_2$.

In the present paper, we will bring two contributions. Firstly, in Section 2 and Appendix A, we will present the analysis of model (2) in the full parameter space. We will show how the effects of dispersal β and of the r_i/K_i ratios combine and we will determine the exact conditions under which $N_T^* > K_1 + K_2$ (see Proposition 2). These results have importance in those cases in which model (2) is a relevant description of logistic growth in a patchy environment.

Our second contribution will be to question the general validity of system (2) for modelling a patchy logistic population, using several simple examples. The logistic model is often justified on phenomenological grounds. However, it can also be derived from mechanistic considerations. Depending on the mechanism being considered, we will show that the correct generalization to a patchy situation is not necessarily represented by model (2) and that the equilibrium total population can be different from that predicted by this model. More precisely, we will show in Section 3 (with Appendix B) and in Section 4 (with Appendix C) that the patch coupling (2) is incorrect in models in which logistic growth is due to resource exploitation, while it is correct in a model in which logistic growth arises from agonistic inter-individual interactions (see Section 5).

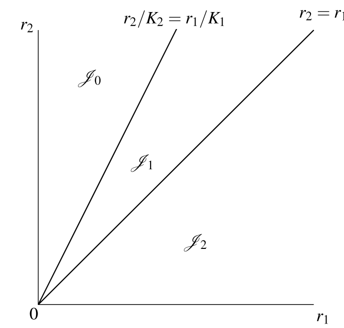

Fig. 1. Qualitative properties of model (2). In $\mathscr{J}_0$, patchiness has a beneficial effect on total carrying capacity. This effect is detrimental in $\mathscr{J}_2$. In $\mathscr{J}_1$, the effect is beneficial for lower values of the migration coefficient β and detrimental for the higher values. Note that, because of the assumption $K_1 \leq K_2$, the two oblique lines cannot be reversed. See text in Section 2 for additional explanations.

2. Theoretical analysis of the standard two-patch logistic model

In this section, we summarize some of the properties of the standard model (2). Formal proofs are given in the Mathematical Appendix A.

As already mentioned in the Introduction, with no dispersal ($\beta = 0$), each patch equilibrates at its own carrying capacity and the total equilibrium number of individuals is just the sum of the carrying capacities: $N_T^* = K_1 + K_2$. This remains true with dispersal ($\beta > 0$) if the two carrying capacities are identical. However, if the carrying capacities are not identical ($K_1 < K_2$), the equilibrium densities are such that

$$K_1 < N_1^* < N_2^* < K_2, \tag{5}$$

meaning that, in general, $N_T^* \neq K_1 + K_2$ (see Proposition 2 in Appendix A).

In particular, the total equilibrium population N_T^* can be *greater* than the sum of the carrying capacities. In the Introduction, we mentioned Freedman and Waltman's result in the case of perfect mixing ($\beta \to \infty$) (Eqs. (3)–(4)). This can also occur with imperfect mixing as, for example, if $r_1/K_1 < r_2/K_2$ (with $K_1 < K_2$). In this case, as shown in Appendix A,

$$N_T^* > K_1 + K_2, \quad \text{as soon as } \beta > 0. \tag{6}$$

Note that, if migration is asymmetric ($\beta_1 \neq \beta_2$), then it is possible to have $N_T^* > K_1 + K_2$ even in the case $K_1 = K_2$ (Poggiale et al., 2005).

Appendix A gives the full mathematical analysis of the equilibrium properties of the coupled logistic model (2). The main qualitative results are summarized by Fig. 1. Depending on the inequalities between r_1 and r_2, and between r_1/K_1 and r_2/K_2, three different domains must be considered in the parameter space $r_1 \times r_2$. We define $\mathscr{J}_0$ by the condition $r_2/K_2 \geq r_1/K_1$, $\mathscr{J}_2$ by the condition $r_2 \leq r_1$, and $\mathscr{J}_1$ by the condition $r_2/K_2 < r_1/K_1$ and $r_2 > r_1$.

The effect of patchiness and migration is different in the three domains. In $\mathscr{J}_0$, this effect is beneficial: N_T^* is always greater than $K_1 + K_2$. In $\mathscr{J}_2$, the opposite is true: patchiness is detrimental since N_T^* is always smaller than $K_1 + K_2$. In $\mathscr{J}_1$, the effect of patchiness depends on the migration rate: it is beneficial at lower values of the migration coefficient β while this effect becomes detrimental at high values. This is illustrated by Fig. 2, in which the total equilibrium abundance N_T^* is plotted as a function of the migration rate β. Depending on the choice of parameter values (given in Table 1), this figure shows three different example patterns, belonging respectively to $\mathscr{J}_0$, $\mathscr{J}_2$, and $\mathscr{J}_1$.

Fig. 2(a) is an example response in $\mathscr{J}_0$: as soon as there is some migration ($\beta > 0$), the global carrying capacity N_T^* is greater than $K_1 + K_2$. In Fig. 2(b), we show an example response in $\mathscr{J}_2$: the total