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To connect or not to connect isolated patches

Daniel Franco ^{a,*}, Alfonso Ruiz-Herrera ^b^a Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Nacional de Educación a Distancia (UNED),

c/ Juan del Rosal 12,28040 Madrid, Spain

^b Bolyai Institute, University of Szeged, EPIDELAY Research Group, Szeged, Hungary

HIGHLIGHTS

- Short and long term dynamics of a discrete population system are studied.
- Results show that increasing migration rate can increase/decrease total population size.
- We characterise the systems for which migration boosts total population size.
- Consequences in conservation strategies (corridors and no-take zones) are discussed.

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ABSTRACT

Empirical evidence suggests that dispersal can have different effects on the time evolution of a spatially structured population. In this study, we explored the impact of the migration rate in a coupled map lattice system. To capture this impact, we assumed symmetric dispersal and simple dynamics in the local populations. However, we allowed heterogeneity between the patches, including both source–source and source–sink systems. Our results show that this simple theoretical setting has the potential to unify the diversity of behaviours of the total population size observed in previous studies. Indeed, we found that the response of the total population size to migration was non-monotone in source–source and many source–sink situations, thereby suggesting that an increase in the dispersal rate could be related to either an increase or a decrease in the total population size. As we will illustrate, this response provides a possible theoretical explanation of some benefits of control strategies involving spatial considerations as no-take zones. Our study also analyses the impact of the migration rate on persistence, spatial coherence, and initial transients. This was motivated by previous theoretical observations in coupled systems that the rate of migration affects these three aspects. Related to persistence, we rigorously extended a previous result from the linear to the non-linear case. This result essentially states that persistence depends on the stability of the origin. On the other hand, we stress that negative effects due to an increase of the spatial coherence could be neutralised by the unimodal response of the total population size. Finally, the study of the initial transients, which is relevant for interpreting experimental results, highlights that the relationship between the rate of migration and the total population size remains the same even in the transient phase.

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1. Introduction

The distribution of populations over space and the movements of individuals within them are relevant factors related to the population dynamics of many species. In fact, theoretical and empirical studies have highlighted the key role of spatial fragmentation in the persistence of endangered species (Grant et al.,

2010; Abbott, 2011; Lampert and Hastings, 2013). Moreover, the impact of spatial considerations has generated much interest in the context of conservation strategy design, such as conservation corridors or marine reserves (Rosenberg et al., 1997; Gaines et al., 2010).

To facilitate the efficient use of conservation strategies, managers need to obtain insights into how movements among different patches affect the total population size, i.e., the number of individuals in all patches. Thus, the main subject of this study is a theoretical investigation of the population dynamics of a single species in a fragmented landscape where each patch is connected

* Corresponding author.

E-mail address: dfranco@ind.uned.es (D. Franco).

by dispersal. We used one of the most popular modelling frameworks employed in metapopulation theory, which is known as a coupled map lattice (CML). Although a CML is considered to be “the simplest possible model that includes spatial effects” (Lloyd, 1995), it has been used to elucidate the biological patterns found in nature or laboratory experiments in previous studies (e.g., Ranta et al., 1997; Dey and Joshi, 2006).

In ecological research, experimental results regarding the effect of spatial fragmentation on the total population size are apparently contradictory. We provide some examples. For a metapopulation of *Drosophila melanogaster*, Dey and Joshi (2006) found that the effects of 10% and 30% dispersal rates on the total population size did not differ significantly. However, for the yeast-like fungus *Aureobasidium pullulans*, the experiments reported by Ives et al. (2004) showed that a considerable increase in the population size occurred as a response to an increased dispersal rate. By contrast, Åström and Pärt (2013) reported that the presence of dispersal corridors in an experimental metacommunity had a negative effect on the abundance of oribatid mites. Thus, providing a theoretical explanation that unifies these experimental results is highly challenging.

To the best of our knowledge, there have been few theoretical studies of the effects of dispersal on the total population size using the CML framework. However, based on a system with environmental stochasticity that caused populations to fluctuate within patches, Ives et al. (2004) showed that three factors increased the total population size: weak density dependence, high environmental variability affecting population growth rates, and the lack of synchrony among the fluctuations in populations. The underlying dynamics of the populations in patches were stable in the sense of being persistent, but the dynamics were chaotic for the parameters used in their simulations. In addition, for a CML with chaotic local dynamics and asymmetric dispersal, Doebeli (1995, Figure 3) presented a numerical example, which showed that the total population size of an equilibrium stabilised by dispersal was larger than the sum of the unstable equilibrium in each patch. However, the asymptotic mean of the total population sizes in the isolated patches may have been greater than the total population size in the connected patches.

To obtain a theoretical understanding of these experiments and to complement the results obtained, we focused on a metapopulation of two different symmetrically connected patches, i.e., an individual moved from patch *A* to *B* with the same probability as one from patch *B* to *A*. We restricted our study to CMLs with simple local dynamics, including both source–source and source–sink systems.

We analysed how migration affected the total population size. Specifically, our results detected a unimodal response, which allowed us to explain the positive, negative, or lack of effect observed in experiments. In addition, we characterised when the presence of a sink can lead to an increase in the total population size in the long term. For exploited species, a consequence of these results is that creating no-take zones could protect the species and simultaneously generate higher economic yields, as it was already reported in Gell and Roberts (2003) and White et al. (2008).

The impacts of an increased dispersal rate on spatial coherence and initial transients were also addressed. On the one hand, to verify whether the benefit of migration (yielding higher total population size) is diluted by the synchronising effects; and on the other hand, to explore whether the benefit of migration can only be observed in a long-time scale far from the time series coming from real experiments. Using the same measure of spatial coherence as Earn and Levin (2006), that is the absolute value of the difference in population size between patches, our results demonstrated that spatial coherence exhibited a U-shaped response relative to migration. Thus, low migration promotes spatial coherence whereas large rates

reduce the degree of synchrony. As a consequence, the effects of dispersal on spatial coherence and the total population size may balance each other in some situations. Finally, our numerical experiments showed that when the total population size was increased by migration, the initial transients did not appear to change this effect in our framework.

2. System description

Our metapopulation comprises two connected subpopulations (*A* and *B*) with discrete dynamics, i.e., in each subpopulation, the post-breeding population size is determined by a map $f_i(N)$, with $r > 0$ the per capita growth rate and the dependence on N can be nonlinear to consider different types of intraspecific competition. We denote r_A and r_B as the growth rates in patches *A* and *B*, respectively. The value of r_i determines whether patch *i* is a sink ($r_i < 1$), where a population is doomed to extinction if it becomes isolated, or a source ($r_i > 1$). Symmetric dispersal occurs at the beginning of the season, in which density-independent constant fraction $m \in [0, 1]$ of the individuals in each region moves to the other region. Thus, mathematically, this implies the following system:

$$\begin{cases} N_A(t+1) = (1-m)f_{r_A}(N_A(t)) + mf_{r_B}(N_B(t)), \\ N_B(t+1) = mf_{r_A}(N_A(t)) + (1-m)f_{r_B}(N_B(t)), \end{cases} \quad (1)$$

where $N_i(t)$ denotes the population size in patch *i* after dispersal at the beginning of generation *t*. System (1) is perhaps the simplest way to study the effects of dispersal and it has been employed in many previous studies (e.g., Gyllenberg et al., 1993; Hastings, 1993; Lloyd, 1995; Earn and Levin, 2006; Ben-Zion et al., 2010; Dey et al., 2014).

For simplicity, we illustrate our results using two scaled versions of maps introduced in the context of fisheries and which have been used extensively in theoretical ecology: the Beverton–Holt map (Beverton and Holt, 1957),

$$f_r(N) = rN/(1+N), \quad (2)$$

and the Ricker map (Ricker, 1954),

$$f_r(N) = rN \exp(-N). \quad (3)$$

As stressed by Brännström and Sumpter (2005), populations with random spatial distributions and scramble competition exhibit simple unscaled Ricker dynamics. This type of competition for resources is experienced by many species, including most microbes, fishes, invertebrates, and amphibians. By contrast, the unscaled Beverton–Holt dynamics are related to contest competition (Brännström and Sumpter, 2005). Thus, the selected scaled versions encompass the two main forms of intraspecific competition. For the Ricker map, using the scaled version has the technical advantage of covering sink and source situations for the same type of maps (note that for $r < 1$ we have a sink and for $r > 1$ a source, in contrast with the unscaled version which always has a source for $r > 0$). Finally, it is interesting to point out that certain types of density-dependent dispersal in a two-patch discrete system can generate the maps (2) and (3) (Marva et al., 2009).

We focus on simple dynamics in the subpopulations. Specifically, we consider parameters r , which guarantee that the map $f_i(N)$ has only one attracting fixed point. This happens for any positive r for (2) and for $r \in (0, e^2]$ for (3). Obviously, this fixed point is zero if the patch is a sink and a certain positive population size if the patch is a source.

The rescue effect is a concept that is intrinsically linked to metapopulations. The theory of source–sink dynamics predicts that emigration from sources can rescue a population from extinction in the sinks (Pulliam, 1988). System (1) exhibits this

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