

The effect of migration on metapopulation stability is qualitatively unaffected by demographic and spatial heterogeneity

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Abstract

Coupled map lattices (CMLs), using two coupled logistic equations, have been extensively used to model the dynamics of two-patch ecological systems. Such studies have revealed that migration rate plays an important role in determining the dynamics of the system, particularly when the two maps differ in their intrinsic growth rate parameter, r . However, under more realistic assumptions, a metapopulation can be expected to consist of more than two subpopulations, each with its own demographic parameters, which will in part be a function of the environment of that patch. The role of the spatial arrangement of heterogeneous (i.e. with different r values) subpopulations in shaping the dynamics of such a metapopulation has rarely been investigated. Here, we study the effect of demographic and spatial heterogeneity on the stability of one- and two-dimensional systems of 64 coupled Ricker maps with different r values, under periodic and absorbing boundary conditions. We show that the effects of migration rate on metapopulation stability do not depend upon either the precise spatial arrangement of the subpopulations in the lattice, or on the presence of a moderate proportion of vacant (uninhabitable) patches in the lattice. The results, thus, suggest that metapopulation models are robust to variation in spatial arrangement of patch quality and, hence, of demographic parameters. We also show that for any given arrangement of the patches, maximum stability of the metapopulation occurs when the migration levels are intermediate, a result that agrees well with previous studies on two-map CML systems.

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1. Introduction

The role of spatial structuring in shaping the dynamics of populations has received considerable attention from both theoreticians and experimentalists (for comprehensive reviews, see Hanski, 1999; Hanski and Gaggiotti, 2004). Coupled map lattices (CMLs), consisting of two or more simple discrete maps

coupled by migration, have been widely used to model metapopulation dynamics, and such models predict a spectrum of spatiotemporal patterns. The simplest form of a CML consists of two one-dimensional maps, such as the logistic or the Ricker equation, connected by migration, and such CMLs have been studied extensively using both analytical and numerical methods (Gyllenberg et al., 1993; Hastings, 1993; Kendall and Fox, 1998). In symmetrical two map CMLs (i.e. both maps have the same value of the intrinsic growth rate parameter, r) using the logistic map, it was seen that when the rate of migration is low, the two patches behave as though their dynamics are independent, whereas for high levels of migration the

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system behaves as though it were a single patch (Hastings, 1993). However, for moderate levels of migration, there are regions in the parameter space where simple dynamics (limit cycles) can be observed even in systems where the r value is high enough to yield chaotic dynamics in a single patch (Hastings, 1993; Gyllenberg et al., 1993). This pattern of effects of migration rate on CML dynamics remained qualitatively unchanged when the two maps were made asymmetric (i.e. differed in the values of the growth rate parameter, r). Kendall and Fox (1998), inter alia, made a detailed numerical investigation of the asymmetric case for different rates of migration. They found that high levels of migration (>0.25), together with differing growth rates in the two maps, led to only in-phase attractors. However, under low rates of migration (<0.25) and different growth rates in the two maps, both in-phase and out-of-phase dynamics were possible. There was also a qualitative change in the pattern of the dynamics at intermediate levels of asymmetry between the maps (Gyllenberg et al., 1993; Kendall and Fox, 1998).

In real metapopulations consisting of more than two subpopulations, considerable variation in demographic and environmental parameters is expected among subpopulations occupying different patches. Moreover, it is possible that differing patterns of environmental heterogeneity across patches can give rise to corresponding patterns in the spatial arrangement of demographic parameters among subpopulations. If such spatial patterns have major effects on metapopulation dynamics, it would constrain the applicability of models that do not explicitly consider variation in the spatial arrangement of demographic parameters among subpopulations occupying different patches. However, in such a case, given that most real metapopulations are expected to consist of multiple patches, the number of possible combinations to take into account would become unmanageably high. This important issue has not been addressed in the past: most previous studies on multi-patch metapopulations assume that all the patches have similar parameter values (e.g. Kaneko, 1987, 1989; Hassell et al., 1991; Rohani and Miramontes, 1995; but see also Singh et al., 2004). Given that the variation in the growth rate parameter r between subpopulations affects the nature of the dynamics in two-map CMLs, we decided to investigate the effect of different spatial arrangements of subpopulations varying in r (demographic heterogeneity) on the interplay between migration rate and metapopulation dynamics in multi-patch CML models. We also examined whether introducing a moderate proportion of vacant (uninhabitable) patches in the lattice (spatial heterogeneity) affected the interaction between migration rate and metapopulation dynamics.

2. The model

We modeled subpopulation dynamics with the Ricker equation (Ricker, 1954),

$$n_{t+1} = n_t \exp(r(1 - n_t/K)), \quad (1)$$

where n_t represents the population size at time t , and r and K refer to the intrinsic per capita growth rate of the subpopulation and carrying capacity of the patch, respectively. The behavior of this map has been extensively studied and it is known that the qualitative nature of its dynamics depends solely on the parameter r (May and Oster, 1976). This map is a close relative of the logistic map and can show chaotic behavior for r values higher than 2.692. We studied the behavior of metapopulations consisting of 64 coupled Ricker maps arranged in either a one- or a two-dimensional array, with each map having a different value of r . Every generation, after reproduction, a constant fraction (m) of each subpopulation emigrates and gets distributed equally into the neighboring patches. In the one-dimensional case, the patches were assumed to be arranged linearly with the periodic boundary condition (i.e. on the periphery of a circle), with migration possible only between immediate neighbors. Thus, the population size for any patch j in generation $t+1$ was given by

$$n_{t+1,j} = (1 - m)n_{t,j} \exp(r_j(1 - n_{t,j}/K)) + 0.5m(n_{t+1,j-1} + n_{t+1,j+1}), \quad (2)$$

where $n_{t,j}$ is the population size in the j th patch at the t th time step, r_j the maximal intrinsic growth rate of the population in the j th patch, K the carrying capacity of the patch (assumed to be same for all patches), and m the migration rate ($0 \leq m \leq 1$).

The size of the entire metapopulation at time t was given by

$$N_t = \sum_{j=1}^J n_{t,j}, \quad (3)$$

where J was the total number of patches in the metapopulation. Similarly, in the two-dimensional case, the 64 patches were assumed to be arranged on a 8×8 square grid with migration possible between the four nearest neighbors under periodic boundary condition (i.e. on the surface of a torus).

In this study, we simulated three different kinds of metapopulations differing in the way in which r varied across the subpopulations: (1) linear, wherein the r values of the subpopulations increased linearly, (2) alternate, where alternate subpopulations had high and low r values, and (3) random, in which the subpopulations with different r values were distributed randomly on the array. Many simulations, with different ranges of possible r values of the subpopulations, were carried out for each of the three types of metapopulation. The mean

r of the metapopulations, averaged across subpopulations, ranged from 2.25 to 4.95 in different simulations, with the r values assigned to the subpopulations in any one simulation having a range of 1 centered symmetrically around the mean (i.e. $\text{mean} \pm 0.5$). The r values of the subpopulations were increased in steps of $1/J$, where J was the total number of patches in the metapopulation. The values of K ($= 600$) and initial population size, $n_{0,j}$ ($= 100$), were kept constant for all the subpopulations. In case of the random arrangement of r values, we ran several simulations but failed to detect any qualitative differences among the results generated and hence present here a randomly chosen set of figures for the relevant migration rates.

In the case of the two-dimensional lattices, we also investigated the effect of spatial heterogeneity on the interplay between migration rate and metapopulation dynamics. Spatial heterogeneity was introduced by designating certain randomly chosen patches in the lattice as voids, which can be thought to represent uninhabitable patches. Immigrants were assumed to be capable of reaching such patches, but were not permitted to reproduce there. Consequently, in the subsequent generation, no emigration from these voids would occur. The presence of a void in the lattice, thus, considerably affects the pattern of migration in the patches surrounding it. While it is clear that introducing an arbitrarily large number of voids will alter the dynamics of a metapopulation in such models, our purpose was to examine the effects of small to moderate

levels of spatial heterogeneity on the interplay of migration and metapopulation dynamics. Hence, we considered only the effect of introducing between two ($\sim 3\%$ of patches) and ten ($\sim 16\%$ of patches) voids in the 64 patch metapopulations.

All programs were written in QBASIC v 4.5 and run on a Pentium III PC. In each individual simulation, Eq. (2), or its equivalent in the two-dimensional cases, was iterated for 1000 time steps, the first 900 values were discarded as transients, and the values of N_t (Eq. (3)) for the remaining 100 generations were recorded. Many such simulations, differing in the mean r value used, were run for each combination of migration rate \times patch arrangement, and the metapopulation size data (N_t) from all simulations of a given migration rate \times patch arrangement combination are plotted in Figs. 1–5 as a function of the mean r for that set of simulations. These figures, thus, represent bifurcation diagrams for metapopulation size for different migration rate \times patch arrangement combinations. We stress that our primary interest in this study was to examine the effect, if any, of patterns of demographic and spatial heterogeneity on the interplay of migration rate and metapopulation dynamics. Consequently, our focus is on total metapopulation sizes and their dynamic behaviour under different migration rate \times patch arrangement \times r combinations. We are not, at this point, interested in examining the possibility of localized patterns of spatial synchrony in these systems, although we appreciate the importance of such patterns in understanding the

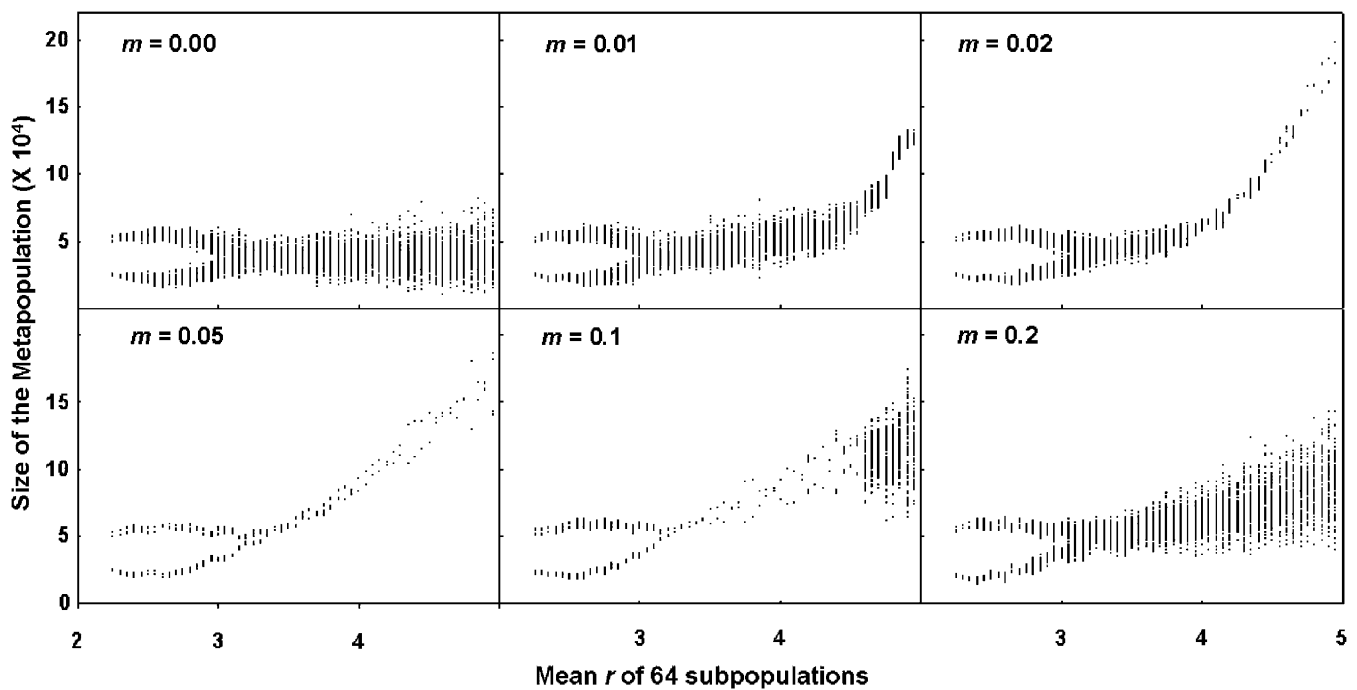


Fig. 1. Behavior of the system when r increases linearly across patches, in a one-dimensional array. m refers to the fraction that migrates each generation to the two neighboring patches. See text for more details.

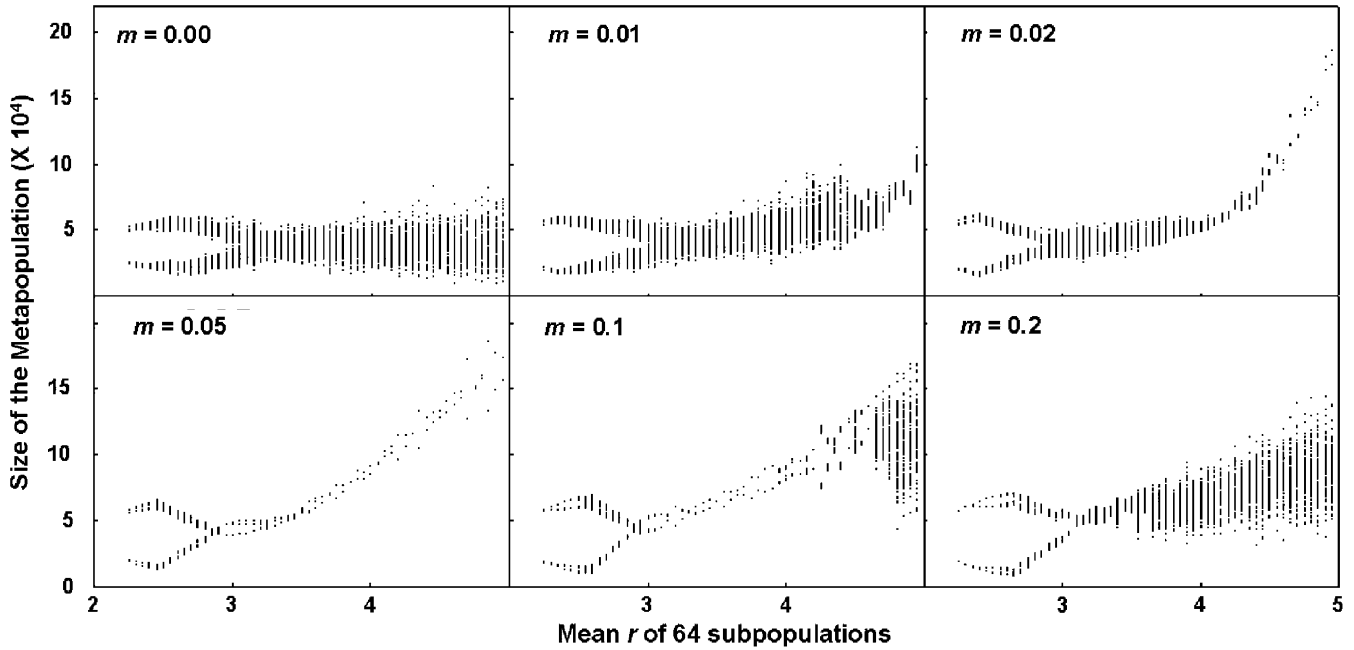


Fig. 2. Behavior of the system when r values alternate between high and low values across patches, in a one-dimensional array. See text for more details.

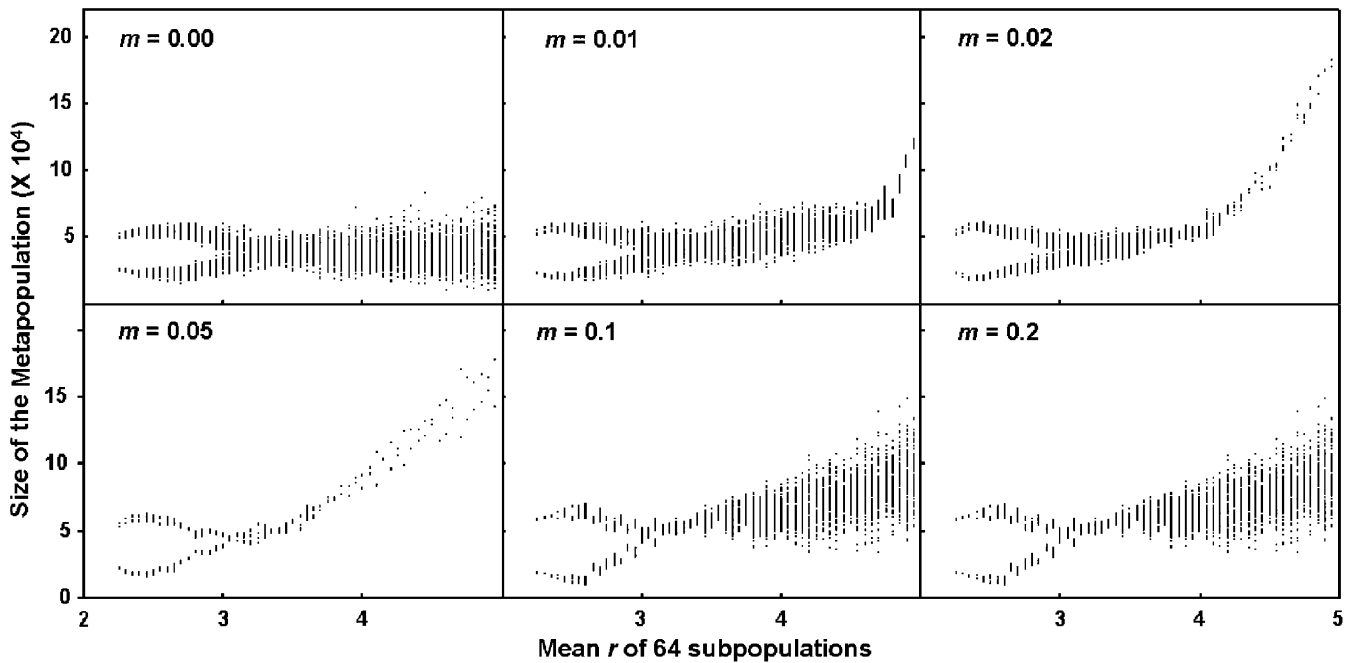


Fig. 3. Behavior of the system when r values are arranged randomly across patches, in a one-dimensional array. See text for more details.

population ecology of spatially structured systems (Mueller and Joshi, 2000; Singh et al., 2004).

3. Results and discussion

The bifurcation diagrams of the metapopulations (Figs. 1–4), with the mean r as the bifurcation

parameter, reveal that the precise spatial arrangement of the subpopulations with heterogeneous r does not lead to major qualitative differences in the dynamics of the system for any migration rate. Moreover, there is not much difference in the behavior of the system whether we consider a one-dimensional or a two-dimensional lattice. Although Figs. 1–4 were plotted for 64-patch metapopulations, the results also hold for

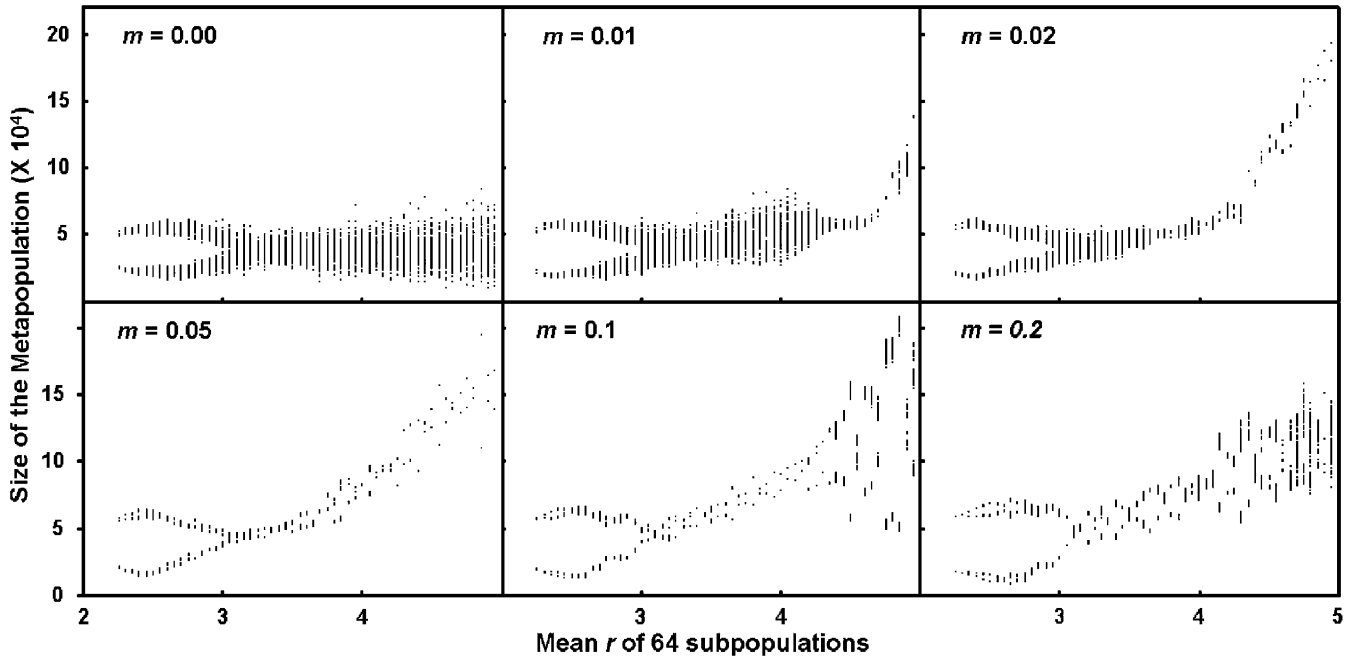


Fig. 4. Behavior of the system when r values are arranged randomly across patches, in a two-dimensional array. Note that we have presented only the random case here, as the nature of the dynamics were similar for the linear and alternate arrangements of r . See text for more details.

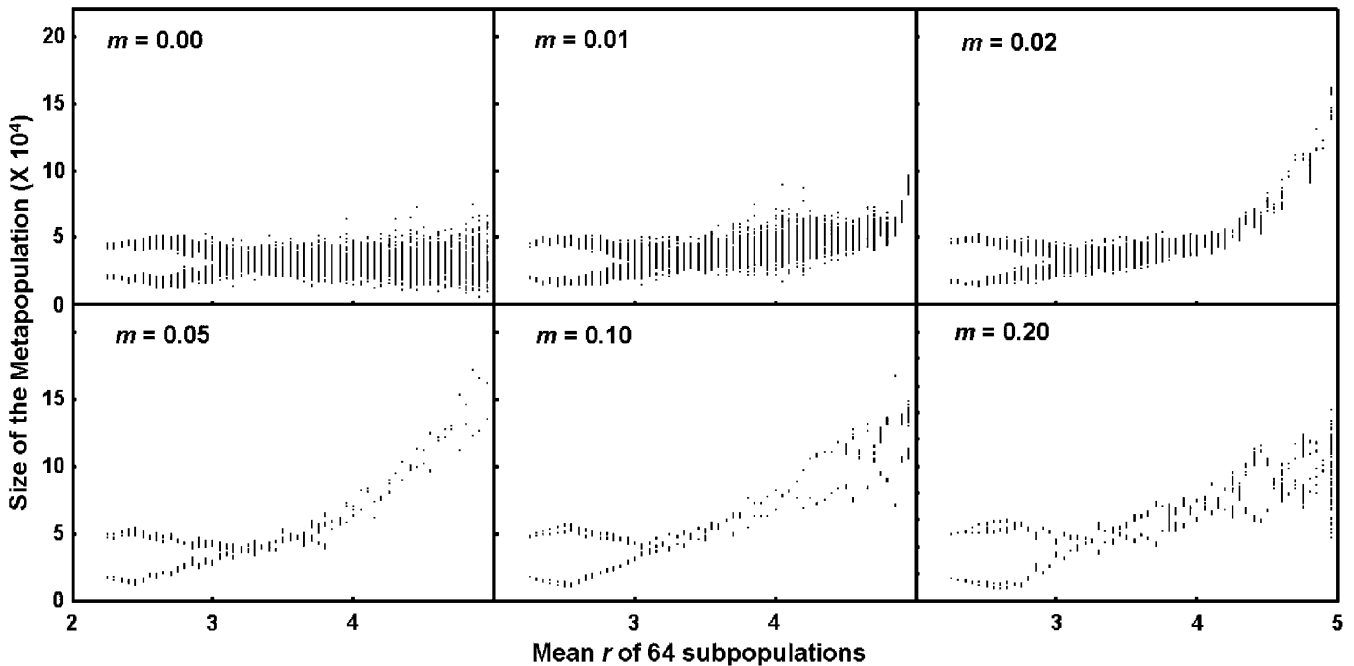


Fig. 5. Behavior of the system when ten voids are introduced at random positions in a two-dimensional lattice with random arrangement of r values. Note that voids were introduced at the same positions for simulations at different values of m . See text for more details.

metapopulations with a smaller number of patches (results not shown), as well as for cases when absorbing boundary conditions were applied (results not shown). We also note that even different random arrangements of the 64 patches failed to produce any discernible

difference in the pattern of the dynamics of the metapopulations. In other words, the interaction of migration rate with the average growth rate (r) of the metapopulation is independent of demographic heterogeneity, or the spatial arrangement of subpopulations

with different r values. Introduction of spatial heterogeneity in the form of voids (uninhabitable patches) also had no discernible qualitative effect on the dynamics of the model metapopulations (Fig. 5), suggesting that, at least for the functional form of the model and proportion of uninhabitable patches used here, spatial heterogeneity does not affect the gross dynamics of metapopulation size, and how it is affected by migration rate. It has earlier been shown, albeit for a different class of model, that introducing even a small number of voids into a CML can promote asynchrony among subpopulations (Singh et al., 2004). Unfortunately, Singh et al. (2004) did not report the effect of introducing voids on the interplay between migration rate and metapopulation dynamics, making a detailed comparison of our results and those of Singh et al. (2004) difficult.

Overall, our results are reassuring because they suggest that the predictions of some typically used models of metapopulation dynamics are likely to be quite robust with regard to the different spatial arrangements of patches with varying demographic parameters, or vacant patches. Such robustness makes results from metapopulation models with arbitrary spatial distribution of demographic parameters generalizable to real ecological scenarios. Whether the same robustness with regard to metapopulation size dynamics is observed for other types of metapopulation models, utilizing different functional forms to represent subpopulation dynamics, is a potential avenue of future work with important implications for application-oriented modeling.

The other observations from our study are similar to those observed in case of two-patch CMLs (Gyllenberg et al., 1993; Hastings, 1993; Kendall and Fox, 1998). In case of zero migration (Figs. 1–4), all patches behave independently, the metapopulation as a whole shows complex dynamics, and the range of fluctuation of the population numbers is high. For low values of mean r , the population size N_t does not settle into limit cycles, and all values settle down to two distinct bands. Although in a mathematical sense, the system seems to be exhibiting a very high period cycle, or even chaos, the statistical periodicity (sensu Turchin, 2003) of the system at this point is likely to be much lower. This is because the attractor, at such values of r , often consists of distinct regions that are visited by the trajectory in turn, rendering the system statistically indistinguishable from one exhibiting low period limit cycles with some amount of noise (Turchin, 2003). As the mean r increases, the two bands come closer and finally merge. At this point, the statistical periodicity of the system is considerably higher and, hence, the stability of the system is reduced. With further increase in mean r , N_t fluctuates extensively, although remaining limited to a more or less defined range. As the migration rate is increased from

1% to 5%, the range of fluctuation of N_t gets reduced at low values of mean r , whereas for higher values of mean r , the system settles into simple limit cycles. However, in case of the one-dimensional array, as the rate of migration increases from 5% to 20%, the system reverts back to the behavior shown in the case when there is no migration (Figs. 1–3). This is probably because by then the system is coupled strongly enough to behave more or less like a single patch (Hastings, 1993). While the same general pattern holds for the two-dimensional case (Fig. 4) too, the reversion to dynamics similar to the zero migration case happens at a higher rate of migration. Thus, the observation that intermediate rates of migration beget higher stability (Hastings, 1993; Gyllenberg et al., 1993) seems to be borne out in the multi-patch case too.

One issue that also merits some discussion here is that of transients. The figures presented in this work were generated by discarding 900 time steps. It is known that sometimes CMLs can lead to very long transient behaviors or supertransients (Hanski, 1999). However, it has been shown, albeit using a model other than the Ricker equation, that the range of conditions under which supertransients occur is fairly narrow (Labra et al., 2003). To be on the safe side, we iterated a randomly chosen subset of the simulations for 10,000 time steps, and plotted only the final 100 values. The resulting figures were indistinguishable from the ones presented in this study. Moreover, it has often been argued that the time-scales under which real populations exist are probably much shorter than the model-predicted time required to reach the equilibrium state. Thus, at least sometimes, transients can be of greater value in ecology than the equilibrium behavior (for a review of this issue, see Hastings, 2004).

To summarize, we show that over a large range of mean intrinsic per capita growth rates (r), the precise spatial arrangement of patches with varying r , or of vacant uninhabitable patches, does not seem to have major qualitative effects on either metapopulation stability, or how the metapopulation dynamics is affected by migration rate. In this study, unlike many previous ones (Gyllenberg et al., 1993; Hastings, 1993; Kendall and Fox, 1998), we used the Ricker equation for modeling subpopulation dynamics. The Ricker equation is generally considered a better model for biological populations than the logistic, partly because it cannot take negative values. Moreover, it is known to give a better fit than the logistic to real life data of the dynamics of several populations (Sheeba and Joshi, 1998). If the pattern of results reported here holds for other more complex and realistic models of population growth, then we may be able to rule out spatial configuration of patch quality as a major factor in the determination of the gross dynamic behaviour of metapopulations.

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