EFFECTS OF DISPERSAL PATTERNS ON POPULATION DYNAMICS AND SYNCHRONY

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             parameter, the intrinsic rate of increase r. Dispersal is assumed to be global
             and dispersal rules explored here include a pattern where a constant fraction of
             every local population disperses in each generation. In addition, we study the
             effects of another density-independent and three density-dependent dispersal
             rules. We also consider asymmetrical dispersal and the presence of
             environmental heterogeneity. According to our results, the effects of density-
             independent and density-dependent dispersal rules do not show any consistent
             difference. However, we found that both population dynamics and the level of
             synchrony differ markedly between two and a larger number of local
             populations. For two patches different dispersal rules give very versatile results,
             whereas for a larger number of local populations the dispersal patterns produce
             qualitatively similar dynamics. For example, for the values of r yielding stable
             or periodic dynamics in a single population, the dynamics do not change when
             the patches are coupled with dispersal. In addition, for the values of parameter
             r producing chaotic dynamics in a single population, dispersal has a stabilizing

effect on the dynamics. Increasing r may destabilize the dynamics, but increasing the asymmetry of dispersal or assuming environmental heterogeneity again stabilizes the dynamics. High intensity of dispersal does not guarantee synchrony in fluctuations of local populations. The level of synchrony depends also on dispersal rule, the number of local populations and intrinsic growth rate.

Effects of dispersal patterns on population dynamics and synchrony

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1 Introduction

Theoretical research on animal populations has mainly focused on temporal variations in the abundance of populations (Royama 1992). However, during the recent decade interest in the spatial aspects of populations has substantially increased. The cause for this interest is mainly the fragmentation of landscape due to human activities and the threat that it causes to the survival of species (Bascompte & Solé 1998). At present, some of the intensively studied topics are the effects of space on population dynamics (Udwadia & Raju 1997; Amarasekare 1998; Doebeli & Ruxton 1998; Kendall & Fox 1998), extinction (Allen *et al.* 1993; Heino *et al.* 1997) and evolution (Jánosi & Scheuring 1997; Johst & Brandl 1997; Travis & Dytham 1998; Travis & Dytham 1999; Travis *et al.* 1999; Ranta *et al.* 2000).

Most of the theoretical work dealing with spatial aspects of discrete-time single-species systems has focused on dispersal where a constant fraction of local populations disperses per generation (Gyllenberg *et al.* 1993; Hastings 1993; Doebeli 1995; Lloyd 1995; Udwadia & Raju 1997; Kendall & Fox 1998). Another density-independent dispersal rule, which is used in some theoretical explorations, is a constant number of individuals immigrating in each generation (McCallum 1992; Stone 1993; Doebeli 1995). The proposed biological justification for this dispersal pattern is that the constant number of individuals represents the part of the population, which is isolated from density-dependent effects. Some analytical results have been derived for two local populations where a constant fraction of the subpopulations disperses in each generation and the dynamics in both patches are described by the logistic model (González-Andujar & Perry 1993; Gyllenberg *et al.* 1993; Hastings 1993; Kendall & Fox 1998). Also the effects of immigration and emigration on dynamics in a single patch have been studied thoroughly (McCallum 1992; Ruxton 1993; Stone 1993; Doebeli 1995).

There are only few theoretical studies on the effects of density-dependent dispersal on population dynamics in discrete-time single-species systems (e.g., González-Andujar & Perry 1993; Ruxton 1996; Amarasekare 1998; Doebeli & Ruxton 1998). Nevertheless, density-dependent dispersal is commonly observed in many vertebrate populations since dispersal is often dependent on social factors and population densities (Hansson 1991 and references therein). Also some invertebrates show density-dependent dispersal (e.g., Kennedy 1956; Cameron & Carter 1979; Fonseca & Hart 1996).

Whether spatial structure stabilizes or destabilizes population dynamics has been under intensive study lately. Here stabilization has to be understood in a biological setting meaning that population dynamics becomes simpler or more regular. It has been shown that adding dispersal to a system of two local populations may convert chaotic dynamics into periodic attractors (González-Andujar & Perry 1993; Gyllenberg *et al.* 1993; Hastings 1993; Doebeli 1995; Lloyd 1995; Udwadia & Raju 1997). However, there exist also counter-examples where dispersal destabilizes population dynamics (Ruxton 1993; Doebeli 1995; Crone 1997; Vandermeer & Kaufmann 1998).

There has not been many investigations on whether the results obtained from two-patch systems could be generalized into a more realistic setting, i.e., a much larger number of local populations (but see the studies on coupled map lattice models, e.g., Rohani *et al.* 1996; Doebeli & Ruxton 1998).

Synchrony in dynamics of two populations indicates that population sizes tend to fluctuate to the same direction. Synchrony is an important concept of spatially coupled populations because it increases the probability of global extinctions (e.g., Allen *et al.* 1993; Ruxton 1994; Heino *et al.* 1997). Famous examples of recorded synchrony in animal populations are boreal small rodent populations (Norrdahl & Korpimäki 1996; Steen *et al.* 1996), red squirrels (Ranta *et al.* 1997), sheep (Grenfell *et al.* 1998) and snowshoe hare (Sinclair *et al.* 1993). The following explanations for the synchrony between populations have been put forward: dispersal among populations (Ranta *et al.* 1995), the so-called Moran effect (Moran 1953a; Moran 1953b; Royama 1992), which is caused by spatially correlated environmental noise and nomadic predators (Ydenberg 1987). At local scale dispersal is assumed to dominate over Moran effect, but at global scale Moran effect is more prominent due to the limited range of dispersal (Hudson & Cattadori 1999).

Our aim here is to study a system of two local populations, which are coupled with different density-independent or density-dependent dispersal strategies. The effects of dispersal on the type of population dynamics and the level of synchrony in local population dynamics are investigated. The results are compared to systems with a larger number of local populations. As a larger number of patches, we have mostly used 25 local populations. Later the findings of two and 25 patches are also compared to those of four patches in order to explore how special the case of two patches really is. Our main interest is in whether the results are qualitatively distinct for different dispersal rules and for a certain number of local populations.

2 The model

In order to study the effects of different dispersal rules on population dynamics and the level of synchrony, we examine a spatially implicit model where local population dynamics are governed by the Ricker model (Ricker 1954)

$$X(t+1) = X(t)e^{r(1-\frac{X(t)}{K})}. \tag{1}$$

Variable $X(t)$ is the population size at time t, r is the intrinsic rate of increase of the population and K is the carrying capacity of the environment. In the base case, the carrying capacity of each patch is set to 100 individuals. The initial values for local populations are drawn from the uniform distribution between 1 and 100.

The timing of different processes is assumed to be the following: first reproduction, then dispersal, and finally census. We presume no dispersal mortality in order to reduce the number of parameters. To get more general results, we also study different
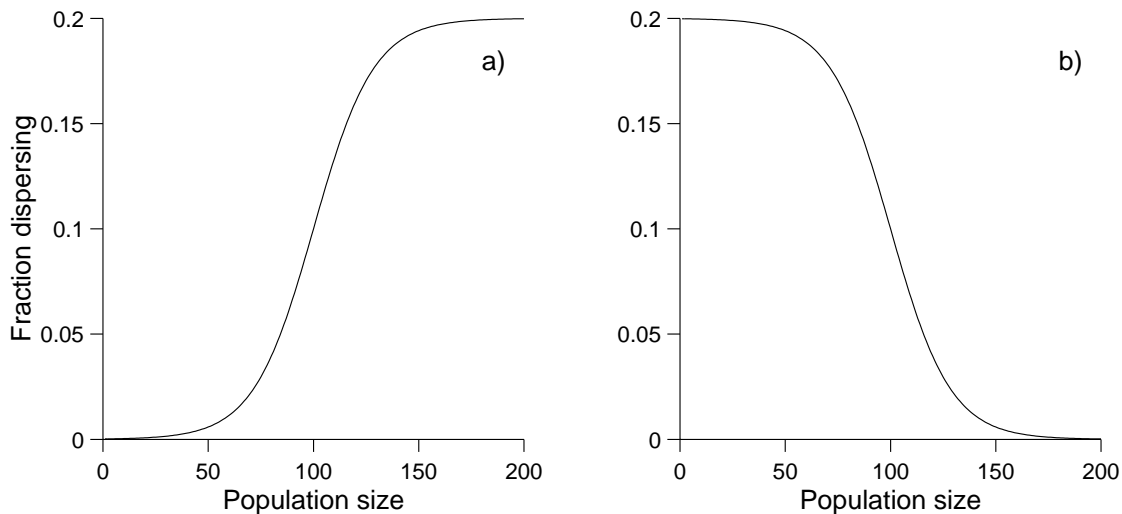
Figure 1: Examples of a) positive (DD1) and b) negative (DD2) density-dependent dispersal rules. Parameter values: $a = 0.2$, $b = 0.07$, $c = 100$, $K = 100$.

intensities of asymmetrical dispersal and spatial heterogeneity, which is incorporated in our model by assuming different carrying capacities for local patches.

We investigate two density-independent dispersal rules: a constant fraction of the population dispersing (DI1) and a constant number of individuals dispersing in each generation (DI2). In addition, three density-dependent dispersal rules are used. In the first one of these strategies (DD1), dispersal rate forms a sigmoidal curve as a function of local population size (Fig. 1a). Positive density-dependent dispersal has been observed for example in northern vole populations (Hansson 1991) and can be related to resource depletion. For DD1-rule the fraction of population size $X(t)$ dispersing at each time step t, $d(X(t))$, is given by

$$d(X(t)) = \frac{a}{1 + e^{b[c - X(t)]}}, \tag{2}$$

where parameter a determines the maximum fraction dispersing. Parameter $b > 0$ describes the steepness of increase in dispersal rate and c determines the inflection point. We have used value $c = K$, which indicates that dispersal rate is half of the maximum $(0.5\,a)$ when the population size equals the carrying capacity.

In the second density-dependent dispersal rule (DD2), dispersal rate decreases with increasing population size (Fig. 1b). This can be obtained from equation (2) when $b < 0$. Negative density-dependent dispersal has been observed for example in desert rodents (Hansson 1991) and can be related to difficulty to find mates.

In the third dispersal rule (DD3), dispersal rate is proportional to the difference between the population sizes in the patches examined. Dispersal rule DD3 differs from the other strategies in a pronounced manner: the organisms are thought to be able to gain knowledge of the population sizes of other patches in addition to their own patch. In a system consisting of two patches, DD3-rule is implemented so that dispersal occurs from the patch with a greater population size and the

fraction dispersing is proportional to the difference between the population sizes. If population size in patch 2 at time t, $X_2(t)$, is larger than population size in patch 1, $X_1(t)$, then the dispersing fraction from patch 2, $d(X_2(t))$, is

$$d(X_2(t)) = a\frac{X_2(t) - X_1(t)}{X_1(t) + X_2(t)}, \tag{3}$$

where parameter a is the maximum fraction dispersing. In a system consisting of more than two local populations, dispersal occurs in the same way except that population size in each patch is compared to the mean size of all local populations.

We examine several values of intrinsic growth rate r which produce different types of dynamics in a single patch without dispersal (for all the dispersal patterns at least $r = 1.0, 1.6, 2.4, 2.6, 3, 4, 5$). To compare the impacts of different dispersal rules on the dynamics, we mostly use bifurcation diagrams. The bifurcation parameters for five different dispersal modes examined here are chosen so that the intensity of dispersal increases with increasing the bifurcation parameter. For a constant fraction dispersal (DI1), we choose the fraction dispersing from patch one as the bifurcation parameter and for a constant number dispersal (DI2), the selected parameter is the number of individuals dispersing from patch one. For all the density-dependent dispersal rules (DD1, DD2 and DD3), the bifurcation parameter is parameter a giving the maximum rate of dispersal. For each value of bifurcation parameter, first 1000 iterations are discarded to eliminate the transient behavior and the next 200 values of population sizes are plotted.

Cross-correlation with lag zero is used to measure synchrony in two local population sizes after the transient phase. For a larger number of patches synchrony is calculated as the average of all pair-wise cross-correlation coefficients. Of course, this method may cause some problems if a part of local populations are in synchrony and some others in asynchrony (Ranta *et al.* 1999). Then the average of the pair-wise cross-correlation coefficients can give misleading results indicating that synchrony in local population dynamics is very small. Therefore, we also calculate the standard deviation of cross-correlation coefficients and in some cases to get more information, we also plot the histograms of the pair-wise cross-correlation coefficients, as suggested by Ranta et al. (1999).

3 Results

In this section we couple local populations with dispersal and study what kind of effects it has on population dynamics and on synchrony in population dynamics. Also different levels of asymmetrical dispersal and environmental heterogeneity are examined for all the studied values of intrinsic growth rate.

Table 1: The effects of dispersal on the dynamics of local populations in a two-patch system for $r \leq 2.69$. Symbol o indicates that dynamics do not change after dispersal, and − and + mean that dispersal may result in stabilized or destabilized dynamics, respectively. Symbols − and + together mean that dispersal can have both stabilizing and destabilizing effects. Symbol o together with − or + indicates that for some values of r, dispersal does not change the dynamics but for some other values of r stabilization or destabilization may occur.

	DI1	DI2	DD1	DD2	DD3
EQUILIBRIUM					
identical patches	o	o	o +	o +	o
asymmetrical dispersal	o	o +	o	o	o
environmental heterogeneity	o +	o +	o	o	o +
PERIODIC					
identical patches	o	+	o	+	o
asymmetrical dispersal	− +	− +	− o +	− +	o
environmental heterogeneity	− +	− +	− o +	− o +	− o +

3.1 Dynamics in stable and periodic region

First we examine dynamics of local populations and consider the intrinsic growth rate values which exhibit equilibrium or periodic dynamics in a single population with the Ricker model, i.e. $r \leq 2.69$.

Two patches. In a system consisting of two patches the results depend somewhat on dispersal rule used (Table 1). For $r < 2$ (equilibrium in a single patch without dispersal), the dynamics are destabilized in a few cases. Quasiperiodic dynamics are observed for DI1 and DD3 when the carrying capacities of the patches differ markedly and dispersal intensity is very high. Moreover, some parameter values in the model with a constant number of dispersers (DI2) produce non-unique dynamics, i.e., qualitative behavior of the system depends on the initial values (Hastings 1993). The possible multiple attractors are not studied in detail in this paper (for more information see Hastings 1993; Lloyd 1995; Udwadia & Raju 1997). DI2-rule can produce more complex dynamics when there is a large number of dispersing individuals. Dispersal patterns DD1 and DD2 can destabilize an equilibrium population size, when the patches are identical and dispersal is symmetrical (Fig. 2a). This occurs for $r \geq 1.8$ (DD1) or $r \geq 1.3$ (DD2) and high intensities of dispersal.

The results for $2 \leq r \leq 2.69$ are more versatile (Table 1). For some dispersal rules coupling two patches together may stabilize or destabilize the dynamics or leave the dynamics unaltered depending on the intensity of dispersal. The bifurcation diagram of a constant fraction dispersal (DI1) for $r = 2.6$ is shown in Figure 2b. In a single patch the dynamics would exhibit a 4-cycle whereas in the case of two local populations increasing the fraction dispersing first produces 4-cycles as in a single population then 2-cycles and eventually equilibrium dynamics. For very large fractions of dispersers, the model produces quasiperiodic dynamics and high-period cycles. The stabilizing effect of this dispersal rule becomes more pronounced for stronger spatial heterogeneity and for more asymmetrical dispersal.

25 patches. The effects of dispersal change dramatically when the number of patches is increased to 25. The dynamics of a single population is passed on to local populations, i.e., for $r < 2$ equilibrium dynamics and for $2 \leq r \leq 2.69$ cyclic dynamics are observed in each patch after dispersal takes place. The only case where this conclusion does not hold is DD2-rule for $1.5 \leq r \leq 2$, when periodic dynamics can be detected. However, also for DD2-rule the dynamics are more regular than in the case of two local populations and equilibrium dynamics are observed until larger intensities of dispersal than for two patches. In consequence, the effects of dispersal on two and 25 patches are qualitatively different and the dynamics observed in two local populations cannot be directly generalized into a system with a larger number of patches.
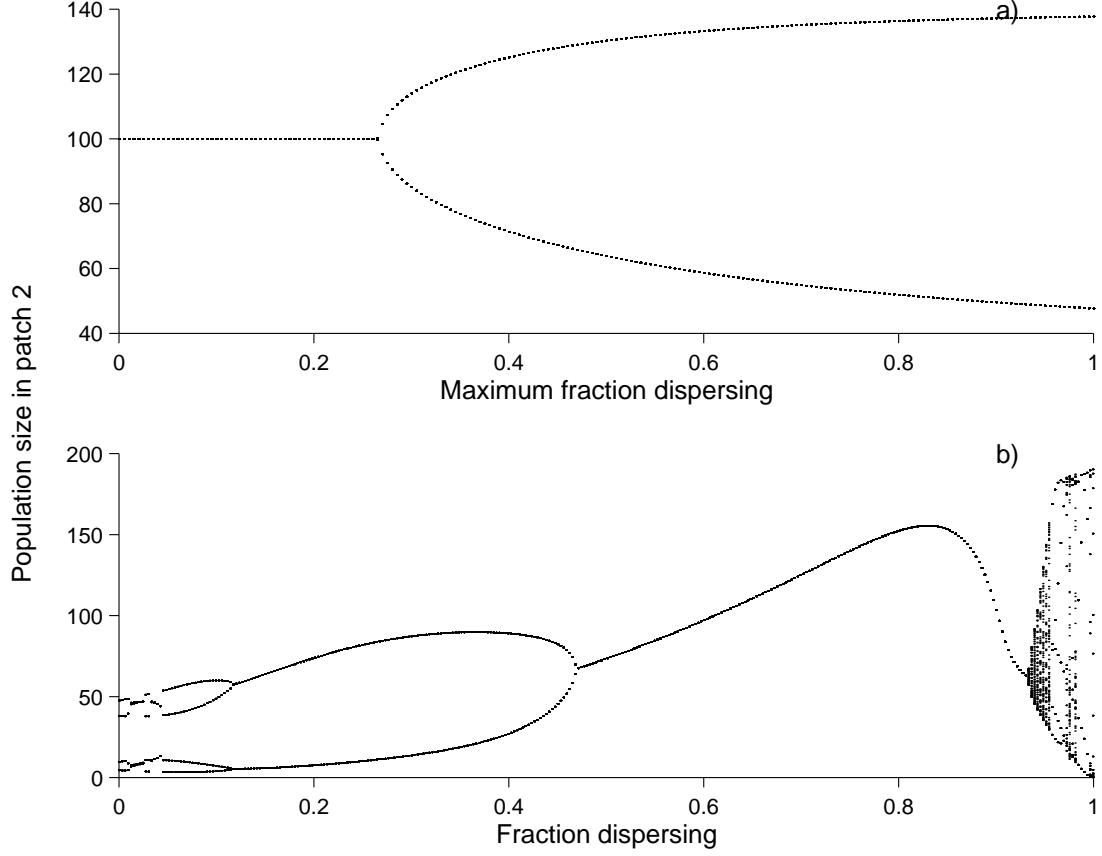
Figure 2: a) Population size in patch 2 in a two-patch system with negative density-dependent dispersal rule (DD2). The equilibrium dynamics are destabilized into a 2-cycle if the maximum fraction dispersing is larger than 0.27. Parameter values: $r = 1.6$, $K_1 = K_2 = 100$ and others as in figure 1. b) Population size in patch 2 in a two-patch system with a constant fraction of population dispersing in each generation (DI1). For a small dispersal rate, coupling the two patches produces 4-cycles as in a single patch but increasing the fraction dispersing can also have both stabilizing and destabilizing effects on the population dynamics. Parameter values: $r = 2.6$, $K_1 = 100$, $K_2 = 25$. The results are qualitatively similar for patch 1.

Table 2: The effects of dispersal on the dynamics of local populations in a two-patch system for $r > 2.69$. Symbols –, o and + as in Table 1.

	DI1	DI2	DD1	DD2	DD3
$r = 3$	–	–	–	–	–
$r = 4$, $r = 5$	o +	–	o +	+	o +
asymmetrical dispersal	– o	– o +	– o	– o	o
environmental heterogeneity	– o	– o +	– o	– o	– o

3.2 Dynamics in chaotic region

Now we examine the intrinsic growth rate values which exhibit chaotic dynamics in a single population with the Ricker model, i.e., $r > 2.69$. The starting point of our studies is the case of $r = 3$. Then we increase the value of the growth rate ($r = 4$ and $r = 5$) and examine whether the results are altered. The number of local populations is the same as in stable and periodic regions: two and 25.

Two patches. The results from two local populations coupled with dispersal are summarized in Table 2. When $r = 3$ all dispersal rules have a stabilizing effect on the dynamics. In a single population, when parameter r is increased, the Ricker model produces more complex dynamics (May 1976). One would expect that this property would be valid also for a larger number of coupled patches, where dynamics are governed by the Ricker model. However, this is not the case for the dispersal rule where a constant number of individuals disperses each generation (DI2) (Fig. 3). Increasing the values of r enlarges the periodic region and new periodic attractors appear for very large numbers of dispersing individuals. More complex dynamics (chaos and high-period cycles) are observed only around carrying capacity. Similar phenomenon has been observed in a case where a constant number of immigration occurs each generation (McCallum 1992). For the other dispersal rules increasing growth rate either destabilized dynamics or dynamics remain qualitatively similar as in the case of $r = 3$.

Asymmetrical dispersal between patches can have a stabilizing effect on population dynamics (Table 2). The only exception is again a constant number dispersal rule (DI2), where asymmetrical dispersal can also destabilize the dynamics: the range of bifurcation parameter values producing periodic dynamics decreases in size. Similar results can be observed when spatial heterogeneity is studied. Differences in carrying capacities can stabilize the dynamics for other dispersal rules than DI2, for which heterogeneity can also destabilize the dynamics (Table 2).
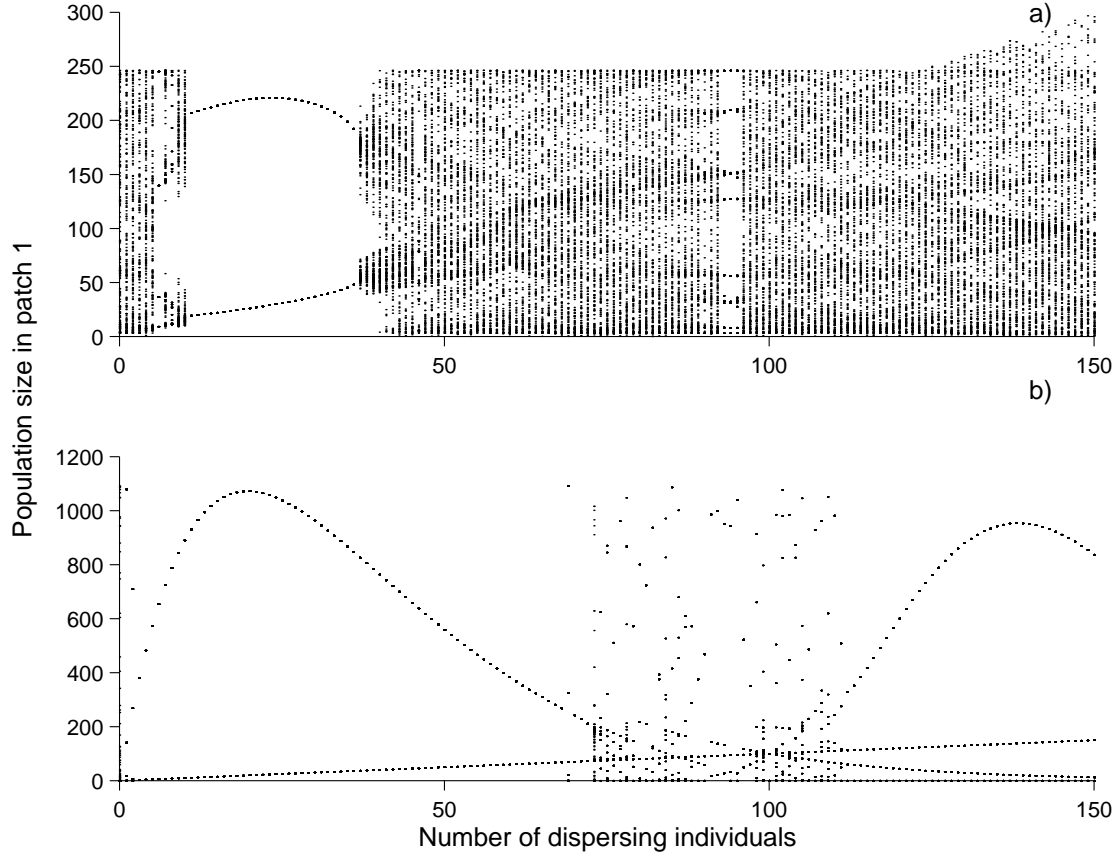
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Figure 3: The population size in patch 1 in a two-patch system with a constant number of individuals dispersing in each generation (DI2) for a) $r = 3$ and b) $r = 5$. Due to symmetrical dispersal and identical patches ($K_1 = K_2 = 100$), the results are qualitatively same for patch 2. Increasing intrinsic growth rate stabilizes the dynamics. This occurs also for other values of r greater than 3.

Table 3: The effects of dispersal on the dynamics of local populations in a 25-patch system for $r > 2.69$. Symbols –, o and + as in Table 1.

	DI1	DI2	DD1	DD2	DD3
$r = 3$	–	–	–	o	o
$r = 4$, $r = 5$	o +	o	o	o	o
asymmetrical dispersal	–	–	– o	– o	– o
environmental heterogeneity	–	–	– o	– o	– o

25 patches. Increasing the number of local populations unifies the results obtained from different dispersal rules, i.e., also DI2 gives similar results as the other dispersal patterns (Table 3). Our results show that dispersal can stabilize the dynamics but increasing the intrinsic growth rate may have destabilizing effects. In several cases, asymmetrical dispersal and spatial heterogeneity produce simpler dynamics than symmetrical dispersal or spatially homogenous systems.

3.3   Synchrony

Two patches. For $r \leq 2.69$ the population sizes with periodic dynamics fluctuate in synchrony for other dispersal rules expect for DD2, where periodic attractors may be out of phase. Due to this asynchrony in local population sizes, total population size is in equilibrium for the whole range of bifurcation parameter values, although local population sizes exhibit 2-cycles for larger values of a (Figure 2a). The synchrony of quasiperiodic dynamics varies between the dispersal rules — dynamics may be asynchronous (DI2, DD1, DD2), there may be no synchrony between the fluctuations of local population sizes (DI1, DD1, DD3) or they may be strongly synchronous (DD1, DD2). For $r > 2.69$ and for small intensities of dispersal the dynamics are very often chaotic and almost no synchrony exists between local population sizes. This is also found for very high intensities of dispersal producing complex dynamics. For intermediate intensities of dispersal exhibiting chaotic dynamics the local population sizes fluctuate strongly in synchrony. However, whether periodic attractors are in phase or out of phase is dependent on dispersal rule and the strength of dispersal.

25 patches. For $r \leq 2.69$ the results depend on the dispersal rule used. For some strategies the dynamics are in synchrony (DI1, DD1) but for some others synchrony does not show any clear patterns — the mean and the standard deviation of the level of synchrony vary for different dispersal intensities (DD3). The latter situation is true also for DI2- and DD2-rules until the intensity of dispersal is very high. Then the fluctuations are in synchrony (Fig. 4). For $r > 2.69$ increasing the intensity
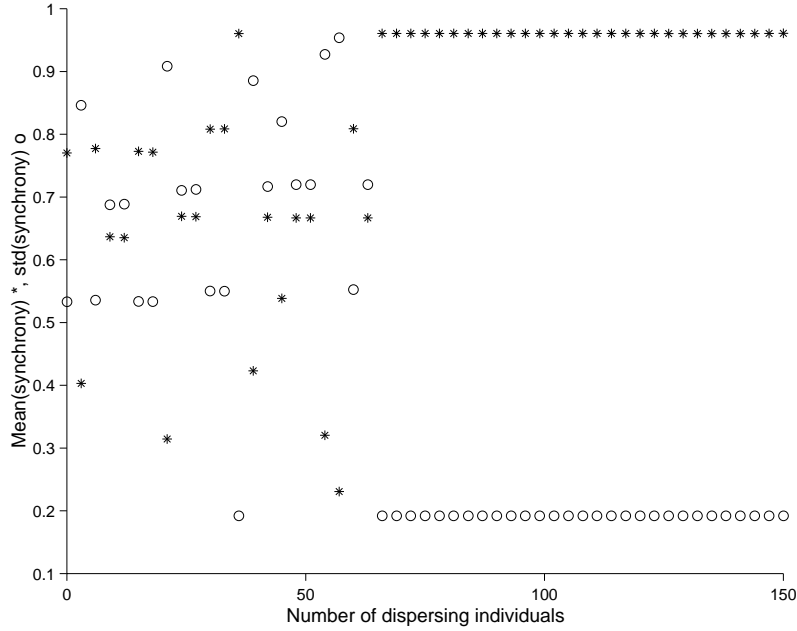
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Figure 4: The means and the standard deviations of pair-wise cross-correlation coefficients of 25-patch system for a constant number dispersal rule (DI2). Parameter values: $r = 2.6$, $K_i = 100$, $i = 1, \ldots, 25$. Although the dynamics in each patch exhibit a 4-cycle, the synchrony between the local populations varies strongly with different numbers of dispersing individuals.

of dispersal also increases the synchrony between the populations. For very high intensities almost all the local population sizes fluctuate in total synchrony.

In summary, there are very few general conclusions that can be drawn from the level of synchrony between the patches for all the dispersal strategies. The results depend strongly on the value of r, dispersal rule, the value of bifurcation parameter (i.e., intensity of dispersal) and the number of local populations.

3.4 Four local populations

One of the main results from previous sections is that outcomes obtained from a system consisting of two local populations coupled with dispersal cannot be directly generalized into 25 patches. Due to this, it is natural to ask: How many local populations do we need until the results start to resemble the ones obtained from 25 patches? In order to study this question, we examine the same cases with four patches as with two and 25 local populations.

The dynamics of four coupled patches resemble quite closely the dynamics of 25 patches. For example, a constant number dispersal rule (DI2) produces qualitatively similar results for $r > 2.69$: increasing the growth rate above 3 does not notable change the dynamics from $r = 3$. In addition, asymmetrical dispersal and

environmental heterogeneity strongly simplify the dynamics. There are some exceptions to this rule: for $2 \leq r \leq 2.69$ the destabilizing effects of dispersal can be observed for DD1 and DD2 dispersal strategies as in two coupled patches. Also the synchrony between the four local population dynamics has similar features as in the case of 25 patches. The only differences are that for $r \leq 2.69$ the means and the standard deviations of the level of synchrony are not as scattered as in the case of 25 patches for dispersal rules DI2, DD2 and DD3. Also for $r > 2.69$ increasing the intensity of dispersal does not strengthen the synchrony for DD3 dispersal rule. To summarize, the results of already four local populations seem to resemble 25 local populations. Thus, the system consisting of two local populations is only a special case and the results obtained from two patches cannot be directly generalized into a larger number of local populations.

4 Discussion

In this paper the effects of density-independent and density-dependent dispersal strategies on dynamics and the level of synchrony in local population dynamics are examined. The results show that there are no general differences between the effects of density-independent and density-dependent dispersal strategies on population dynamics. Amarasekare (1998) came to a different conclusion when he studied a two-patch single-species system with logistic local dynamics and dispersal mortality. He showed that strong density dependence in dispersal amplifies the nonlinearity in the growth rate and, thus, destabilizes the dynamics. Moreover, for weaker density-dependent dispersal the effect of dispersal mortality becomes stronger, which results in more stable dynamics than without dispersal. It is important to notice that according to our study, the increased knowledge of the population sizes of other patches did not cause the dispersal rule DD3 to differ from the other dispersal patterns.

Recently, the interest in synchrony of spatially distributed local populations has strongly risen due to the increased probability of global extinctions caused by strong synchrony. Most of these studies assume that a constant fraction of each local population disperses (DI1) (e.g., Allen *et al.* 1993; Ruxton 1994; Heino *et al.* 1997). However, we have shown that the level of synchrony is very much dependent on the dispersal pattern used. Thus, care should be taken when emphasizing any general conclusion of the effects of dispersal on synchrony based only on a single dispersal rule.

In addition, this study indicates that not only dispersal rule but also the intensity of dispersal and the number of local populations can strongly influence the synchrony between the local fluctuations. Our results confirm previous findings by Udwadia and Raju (1997) that the level of a system parameter such as the growth rate may be very important in understanding the synchrony. Udwadia and Raju came to this conclusion when they observed that for two coupled patches the alteration of the symmetry of growth parameters also led to an equal change of the level of synchrony.

According to our study, the findings obtained from a system consisting of two local populations coupled with dispersal cannot be directly generalized into a larger number of patches. This indicates that the applicability of a large number of theoretical papers dealing with two local populations may be rather limited. However, it is important to keep in mind that for any number of patches larger than two (e.g., four or 25), there is one more assumption to be made: how are the dispersing individuals distributed among the available patches. In this paper, we have assumed global dispersal — distance between the patches has no importance and all the patches are equally available for movement. Similarly, we have chosen not to consider the effect of patch area on the number of immigrants (for an example, see Hanski *et al.* 2000). In future, it would be useful to conduct a similar analysis as the present one with a spatially explicit model.

The general conclusions obtained from this study for growth rate values producing chaotic dynamics in a single population are in accordance with the previous work done on a constant fraction dispersal rule (DI1): dispersal can have a stabilizing effect on the dynamics (e.g., Hastings 1993; Doebeli 1995) and increasing the intrinsic growth rate may produce more complex dynamics also in patchy systems (e.g., Udwadia & Raju 1997). Asymmetrical dispersal and environmental heterogeneity have been shown to stabilize or have no effect on the stability of the dynamics (e.g., Doebeli 1995; Amarasekare 1998). According to our results, the only dispersal rule which does not meet these conclusions is a constant number of individuals dispersing per generation (DI2). For DI2-rule increasing growth rate stabilizes dynamics and asymmetrical dispersal as well as environmental heterogeneity can also destabilize the dynamics. However, these phenomena occur only when two local populations are coupled with dispersal. Increasing the number of local populations unifies the results with other dispersal rules. Udwadia and Raju (1997) have reported that slight changes in the symmetry of the intrinsic rates of increase give very similar dynamics as identical local populations. However, different timing of reproduction and dispersal in two patches can stabilize dynamics (Doebeli 1995). We have not assumed any dispersal mortality but previous studies have shown that dispersal mortality simplifies the dynamics by reducing the growth rate (Ruxton *et al.* 1997; Amarasekare 1998).

In this study, stochasticity is not added to the model in order to keep the setting as simple as possible. We observed that for different dispersal rules coupled local populations with chaotic dynamics may fluctuate in total synchrony. This has previously been shown for a constant fraction dispersal rule (DI1) (Heino *et al.* 1997; Udwadia & Raju 1997). However, there is evidence that chaotic dynamics amplifies external noise and Heino *et al.* (1997) have reported that adding environmental noise to a model exhibiting chaotic dynamics can produce asynchrony in dynamics of local populations and as a result, decrease the probability of global extinctions. Thus, incorporating environmental stochasticity into the models may change the level of synchrony dramatically.

Recently, several theoretical papers have dealt with the consequences of dispersal on population dynamics but empirical work has lagged behind. In a couple of empirical

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studies, the most significant mechanisms which stabilize the yearly fluctuations of population density have been suggested to be density-dependent dispersal and dispersal mortality (Hirano 1993; Sawada *et al.* 1993; Herzig 1995). They are presumed to stabilize the fluctuations by spreading outbreaks over larger areas or decreasing overcrowding. However, more empirical work needs to be conducted to test the hypotheses put forward by theoretical studies.

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