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Impact of Dispersal on the Total Population Size, Constancy and Persistence of Two-patch Spatially-separated Populations

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Abstract. This paper explores by means of extensive numerical simulation how unidirectional and bidirectional symmetric dispersal can affect the mean total population size and the fluctuation range in a two-patch population model described by coupled difference equations. The obtained results show that the response to dispersal varies not only with the type of connection between subpopulations, but also with the intrinsic dynamics in each subpopulation. We find that the mean total population size increases monotonically with unidirectional dispersal from a region with local complicated dynamics to a region with an attracting equilibrium, whereas in the other studied scenarios the response is generically unimodal. Constancy and persistence are considered by relating them to the fluctuation range. Our results show that dispersal is capable of enhancing constancy and persistence only in certain situations. Additionally, we show that multistability affects the behaviour of the mean total population size and its fluctuation range. Hence it can be concluded that, in contrast to other control strategies, only if there is a good knowledge of the local population dynamics, then a modification of the natural dispersal rate between regions might be used as a way to control the size and stability of the population.

Keywords and phrases: population dynamics, spatial fragmentation, dispersal

Mathematics Subject Classification: 92D25, 37N25

1. Introduction

The increasing fragmentation of the natural environment causes more and more species to inhabit heterogeneous regions. These regions are often connected, that is, individuals can migrate from one region to another. Understanding the role of these connections in population dynamics is an important problem in ecology [25]. In addition to a purely scientific interest of this problem, there are also practical implications. For instance, facilitating/hindering the movement of individuals across different regions has been used as an environmental control tool (e.g. ecological corridors, dispersal barriers [8, 12, 32]). Hence, to design and manage these strategies, it is necessary to understand how the modification of the dispersal

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rate affects population dynamics. The main aim of our paper is to contribute to this understanding by numerically exploring the effect of dispersal on the mean total population size and its fluctuation range.

Several mathematical models have been proposed to capture the movement of individuals in a spatially-separated population. One of the simplest among them assumes that the dynamics in each subregion, when it is isolated, can be described by a discrete population map; then, dispersal is incorporated by means of a nonnegative square matrix C in which each element c_{ij} represents the percentage of population moving from patch j to patch i—see the next section for more details. Despite its formal simplicity, this deterministic model has shown an exceptional versatility to explain experiments about the effects of dispersal on stability, synchrony, or extinction risk [6, 13]. Nevertheless, we should stress that the movement of individuals highly matters in aspects not captured by this model as evolution [26] or the spread of diseases [22,29]. For simplicity, many authors have focused on the case of just two single-species subpopulations linked by dispersal—also known as a two-coupled map lattice [2,4,5,7,11,13,17,18,23,24]. In this case, connecting the two supopulations can be done by unidirectional (one subpopulation acts as the donor whereas the other is the recipient) or bidirectional dispersal [4]. Here, we consider a two-coupled map lattice with spatial heterogeneity; i.e. local dynamics in each subregion are different.

Dispersal can largely influence population dynamics in the model we are considering. Linking subpopulations with *complicated* or even *chaotic* local dynamics [31] can create an overall stable equilibrium or cycle [4, 17]. Besides, increasing dispersal enhances synchrony [8], which is considered a dangerous effect for the species because having low population density in both patches simultaneously puts at risk the viability of the whole population. Finally, connecting heterogeneous subregions can create a "rescue effect" [11,14,19]: a subregion where the population would not survive if isolated is permanently inhabited with the help of another subregion. Most of these properties have been shown for specific cases with symmetric dispersal, but the potential interactions between local dynamics and asymmetric dispersal remain almost unexplored [4].

To the best of our knowledge, there are few theoretical studies of the effects of dispersal on the total population size using two-coupled map lattices. In [7], a population with complicated local dynamics in both subregions was considered. There, the author observed that at an equilibrium stabilised by dispersal, the total population size was much larger than the sum of the unstable equilibrium sizes in each isolated subpopulation. On the other hand, Ives et al. [21] showed that three factors increase the total population size: weak density dependence, high environmental variability affecting population growth rates, and the lack of synchrony among the fluctuations in populations. But this was done for a stochastic system. Considering a deterministic model, it was shown in [11] that the total population size generally has a unimodal response to the increase of dispersal. At low rates of dispersal the total population size increases, whereas at higher rates of dispersal the total population size decreases. However, this was only shown for a population with simple local dynamics in both subregions, i.e. assuming that each subpopulation has an equilibrium that is a global attractor.

In this paper, we extend and complete the previous results about the effect of dispersal on the total population size by considering situations in which one of the subpopulations has an attracting equilibrium and the other complicated dynamics. Capturing how the total population size responds to dispersal is hard, mainly because measuring such a size when facing complicated dynamics is difficult. Indeed, for an isolated region with Ricker dynamics [27], it can be proved that the asymptotic mean of the population size converges to the unique equilibrium of the map (even if this equilibrium is unstable) [16], but this is not true for linked regions or other maps. Hence, here the asymptotic mean total population size is numerically approximated. Our results show that the response of the mean total population to dispersal varies not only with the type of connection, but also with the intrinsic dynamics in each subpopulation, making it difficult to give a general recipe for the use of dispersal to manage the size of a spatially-separated population. Nevertheless, in one case (stable recipient and donor with complicated dynamics), increasing dispersal rates seems to increase the mean total population size in all considered configurations.

For metapopulations with complicated dynamics, modifying dispersal rates was proposed as a method for controlling chaos [7]. Controlling chaos aims to stabilise the population dynamics by creating a stable equilibrium or a limit cycle [3, 30, 34]). This was the main goal of [7]. Interestingly, the recent paper [4] shows that the local dynamics and the type of connection play an important role in the effect of dispersal on such a stabilization. But the stability of a population can be related to three main properties [15]: "staying essentially unchanged" (constancy), "returning to the reference state after a temporary disturbance" (resilience), and "persistence through time" (persistence). Another objective of this paper is to measure the effect of dispersal on constancy and persistence, thus complementing the results in [4]. We do it by numerically calculating how the fluctuation range responds to changes of dispersal rates in different scenarios.

Finally, we address the question of whether or not multistability affects the behaviour of the mean total population size and its fluctuation range when both subpopulations have complicated local dynamics. It is well known that the dynamics of a two-patch system may depend on initial conditions (even when the dynamics of the subpopulations have global attractors) [18, 24]. We present two examples in which the response of total population size and its fluctuation range depends on the initial conditions. This suggests that it might be difficult to predict the outcome of control strategies only based on changes of the dispersal rates.

2. Model description

Our model considers two connected patches (A and B) with discrete dynamics. The post-breeding population size in each patch is determined by a map denoted by $f_A(N)$ and $f_B(N)$, respectively. Dispersal occurs after the breeding season according to the dispersal matrix

$$C = \begin{pmatrix} 1-m_A & m_B \\ m_A & 1-m_B \end{pmatrix}.$$

This means that a density-independent constant fraction $m_A \in [0,1]$ of the individuals in subpopulation A moves to subpopulation B and a density-independent constant fraction $m_B \in [0,1]$ of the individuals in subpopulation B moves to subpopulation A. Thus, population dynamics are described by system

$$\begin{cases} N_A(t+1) = (1-m_A)f_A(N_A(t)) + m_B f_B(N_B(t)), \\ N_B(t+1) = m_A f_A(N_A(t)) + (1-m_B)f_B(N_B(t)), \end{cases} \tag{2.1}$$

where $N_i(t)$ denotes the population size in patch i after dispersal at the beginning of generation t.

Without loss of generality, we assume that the dispersal rates satisfy $m_A \geq m_B$. Clearly, if $m_A = m_B = 0$ both subpopulations are isolated. On the other hand, there are two different scenarios of dispersal: unidirectional dispersal ($m_A > m_B = 0$), in this situation region A takes the role of donor and region B of recipient; and bidirectional dispersal ($m_A \geq m_B \neq 0$) which can be symmetric ($m_A = m_B > 0$) or asymmetric ($m_A > m_B > 0$). In this paper, we restrict the dispersal rates m_A and m_B to the interval $[0, 0.5]$. Higher dispersal rates might be categorized as less realistic since individuals in corridors evolve much lower dispersal rates than those in mainland population [33].

As in [4], we consider system (2.1) for Ricker population maps [27]

$$f_A(N) = N \exp\left(r_A(1 - N/25)\right)$$

and

$$f_B(N) = N \exp\left(r_B(1 - N/25)\right).$$

We recall that the dynamics of such Ricker maps depend only on the parameter r_i. There is a global positive equilibrium for $0 < r_i \leq 2$, and a cascade of period doubling bifurcations leads to complicated dynamics as r_i increases from 2.

3. Results and discussion

3.1. Mean total population size and its fluctuation range

We perform various numerical experiments to capture the behaviour of the mean total population size and its fluctuation range. In all of them, one of the subpopulations has an attracting equilibrium and the other has *complicated* dynamics [31]. We select $r_i \in \{1, 1.5, 2\}$ for subpopulations with an attracting equilibrium. Whereas, $r_i \in \{3.65, 3.125, 2.825\}$ is selected for patches with complicated dynamics. This choice of the parameters is primarily motivated by [4]. There, Dey et al. report different responses in the reduction of the complexity of the population dynamics for subpopulations with $r_A \in (3.3, 4)$, $r_A \in (2.95, 3.3)$, and $r_A \in (2.7, 2.95)$ when connected to a subpopulation with an attracting equilibrium [4]. Note that the set $\{3.65, 3.125, 2.825\}$ is formed by the midpoints of the previous intervals.

The mean total population size is approximated using 100 generations after running the system for 3000 generations to remove transient effects, that is by

$$\sum_{t=3001}^{3100} \frac{N_A(t) + N_B(t)}{100},$$

with the initial condition chosen pseudo-randomly in the interval $[0, 50]$ for both subpopulations.

The fluctuation range is approximated using 100 generations after running the system for 3000 generations by

$$\max\{|N_A(t) + N_B(t) - N_A(s) - N_B(s)| : t, s = 3001, \ldots, 3100\}.$$

3.1.1. Unidirectional dispersal

Since we assume that one subpopulation has an attracting equilibrium and the other has complicated dynamics, it is necessary to consider two possibilities: (i) the donor or (ii) the recipient has complicated dynamics.

Figure 1 shows the results obtained when the donor has complicated dynamics. The mean total population size is always favoured by dispersal, in the sense that it is larger for linked regions than for isolated ones regardless of the dispersal rate. Further, the mean total population size increases with dispersal rate and attains its maximum value for $m = m_A = 0.5$ in all the cases. Such an increase could be related to the hydra effect. Essentially, this effect consists in an increase of the population size in response to harvesting (see [1] for a description of the mechanisms producing this effect). Since net emigration acts like harvesting, it leads to an "altered fluctuation" in the donor as the system is forced to a different attractor (see [20, Figure 7] for an example of this behaviour in a different setting). Nevertheless, we point out that the increase of the total population size due to dispersal was also observed in [11] for the Beverton-Holt map, which does not show the hydra effect under harvesting. Therefore, we conjecture that the hydra effect could be enhancing this response, but it is not the main reason for it.

The numerical simulations show that the fluctuation range is much more dependent on the local dynamics, determined by the intrinsic growth-rate parameters r_i, than the mean total population size. Observe that for $r_A = 3.65$ the fluctuation range increases as dispersal rates increase. But for smaller r_A it essentially has a one-humped behaviour. Interestingly, only in one case (corresponding to panel G) there is a significant interval of dispersal rates able to reduce the fluctuation range with respect to that of the isolated patches ($m = 0$). For the other cases, fluctuations are generically increased by dispersal. This suggests that having a donor with complicated dynamics impedes constancy. Now, observe the behaviour of the total population size in the whole period of 100 generations for each dispersal rates (light blue dots). With the exception of panel G, the minimums of those sizes are generically smaller than for the case $m = 0$. Thus, dispersal could be regarded as negative not only for constancy, but also for persistence.

We conclude that unidirectional dispersal with a donor with complicated dynamics is stabilising only for small values of r_A and r_B. In such a case, increasing the dispersal rates improves constancy and persistence at the same time that reduces the complexity of the population dynamics (period-four and

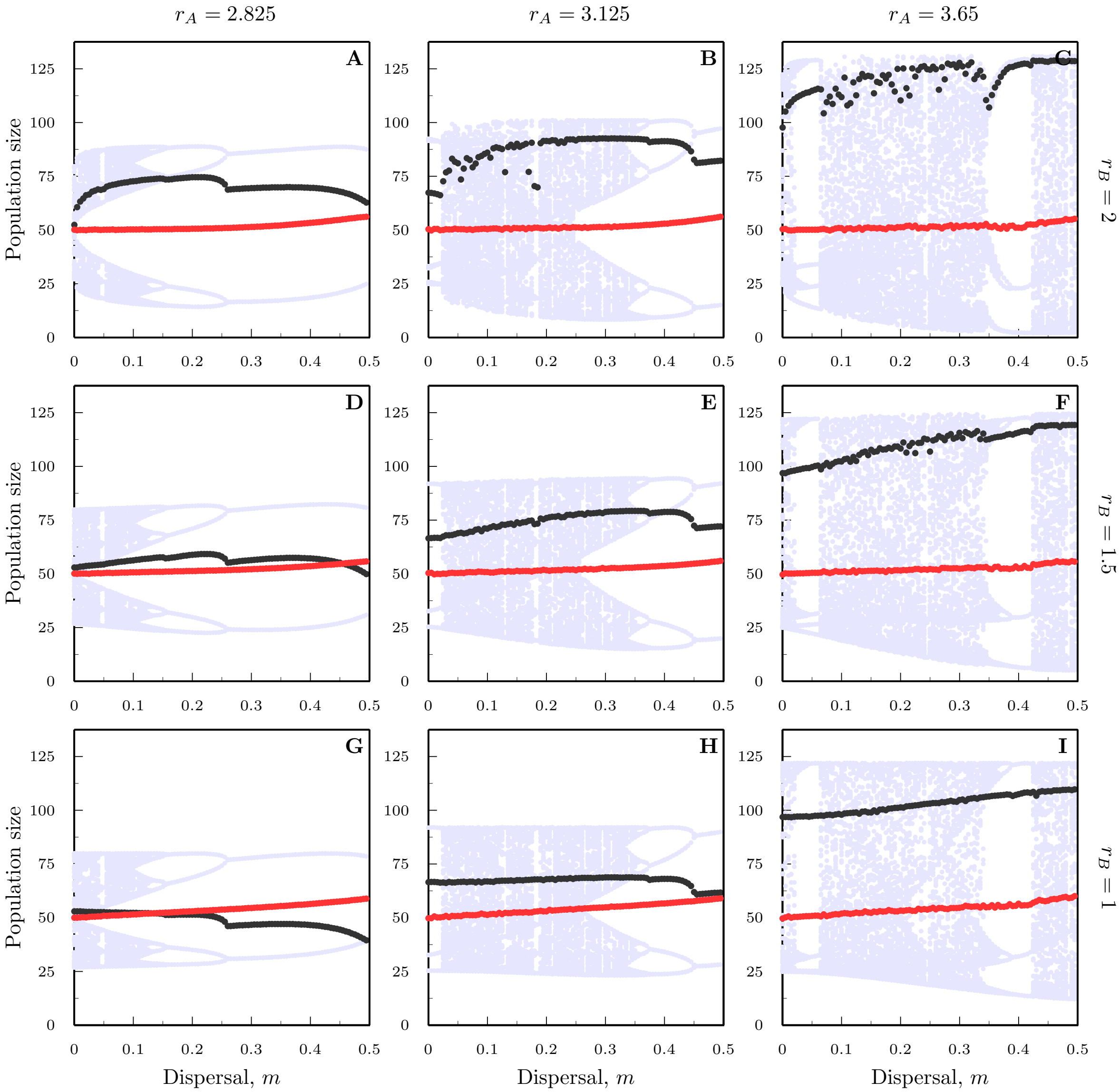

FIGURE 1. Unidirectional dispersal for a donor with complicated dynamics and a recipient with an attracting equilibrium. Panels A-I show nine different configurations with r_A constant in each column (increasing from left to right $r_A = 2.825, 3.125, 3.65$) and r_B constant in each row (increasing from bottom to top $r_B = 1, 1.5, 2$). The mean total population size (red) and its fluctuation range (black) overlie the bifurcation diagram, where the system was run for 3000 generations to remove transient effects, and then the total population size in the next 100 generations was plotted (light blue). See main text for a discussion of the results.

two cycles are stabilised by dispersal after a cascade of period halving bifurcations). Moreover, these stabilising effects coexist with an increase of the mean total population size.

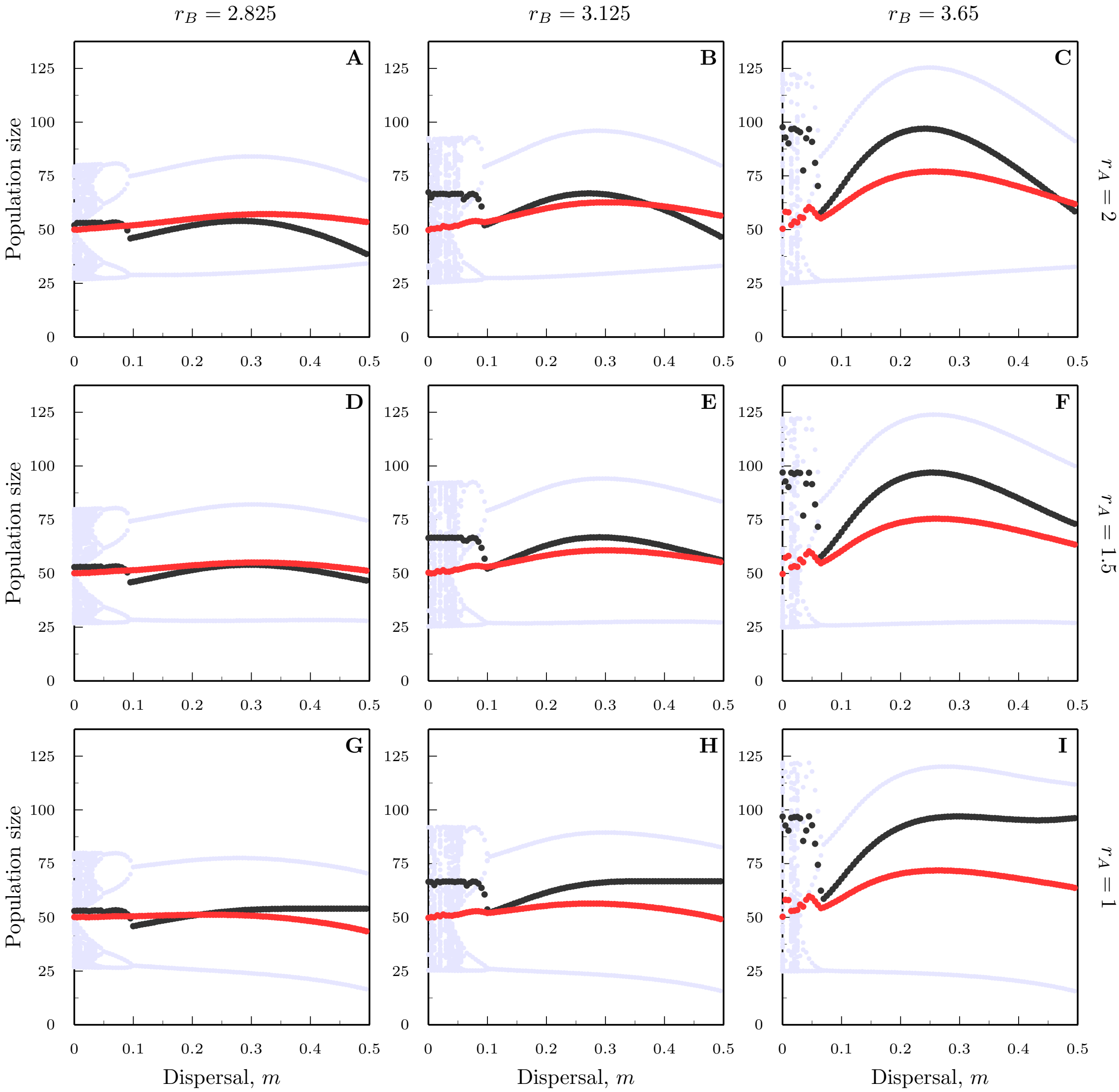

FIGURE 2. Unidirectional dispersal for a donor with an attracting equilibrium and a recipient with complicated dynamics. The mean total population size (red) and its fluctuation range (black) overlie the bifurcation diagram, where the system was run for 3000 generations to remove transient effects, and then the total population size in the next 100 generations was plotted (light blue). See main text for a discussion of the results.

Next, let us consider the case of the recipient having complicated dynamics, which is shown in Figure 2. First, we observe that dispersal is always able to stabilise a period-two cycle, consequently reducing the complexity of the population dynamics. Second, and in contrast with the previous case, the mean total population size is not always promoted by dispersal. Indeed, the mean total population size is smaller for the connected regions than for the isolated regions in panel G with high dispersal rates. Besides, the responses of the mean total population size to an increase of the dispersal rates are essentially one-humped. Thus, an increase of dispersal could be related to an increase or a decrease in the mean total population size. Again, an hydra effect may be enhancing these responses, since the emigration from the donor acts like harvesting and releases that subpopulation from intraspecific competition pressure [1]. We stress that the population size is measured after dispersal in our experiments, and it might be that the consequences on the mean total population size are different if the population were censused after reproduction instead, as it occurs with the "hidden" hydra effects [20].

Contrary to the case of a donor with complicated dynamics, the fluctuation range reduces with respect to that of the isolated patches—consequently constancy improves since a population has greater constancy when it has a lower variation in size over time [15]. This happens in all the configurations, although for different dispersal rates. Therefore, unidirectional dispersal with a donor that has an attracting equilibrium could be used as a stabilising strategy focused on constancy as the adaptive limiter control [9, 10, 28]. On the other hand, the way in which connectivity affects persistence strongly depends on the donor's growth rate parameter. Regardless of the value of r_B, the minimum total population size (over the considered period of 100 generations) decreases with dispersal for $r_A = 1$, stays approximately constant for $r_A = 1.5$, and increases for $r_A = 2$. In the light of these simulations, the optimal response for stability takes place for donors with large parameter r_A, since there are intervals of dispersal rates able to improve (at the same time) constancy and persistence.

3.1.2. Bidirectional dispersal

Here we only present simulations for bidirectional symmetric dispersal. This has the advantage of reducing the two parameters related to dispersal to just one, so we can discuss easily the effects of increasing connectivity as in the previous scenario. This restriction should be considered relatively unimportant after studying the two previous unidirectional dispersal cases since, as stated in [4], *asymmetric dispersal can be viewed as spanning a continuum between the two extremes of unidirectional and bidirectional symmetric dispersal, respectively.*

Figure 3 shows the simulations for bidirectional symmetrical dispersal where subpopulation B has an attracting equilibrium while subpopulation A has complicated dynamics. Dispersal reduces the complexity of the population dynamics provided that r_A and r_B are small enough. In such a case, a positive equilibrium, a period-two cycle, or a period-four cycle are stabilised after a cascade of period halving bifurcations. The only simulation with a different kind of response is the configuration with $r_A = 3.65$ and $r_B = 2$ (panel C). There, increasing dispersal from $m = 0$ produces a series of period halving bifurcations, followed by the stabilisation of period-four and period-two cycles for intermediate values of m. Then, a series of period doubling bifurcations appear, followed by complicated dynamics for higher dispersal rates. This latter effect of dispersal on the population dynamics was already reported in two-patch models when both subpopulations have intrinsically complicated dynamics [2, 4, 17, 18].

The mean total population size is larger for linked regions than for isolated regions in all configurations. This result agrees with the behaviour found in [11], where both subpopulations had an attracting equilibrium and the same type of dispersal as here was considered. Also as in [11], an increase of the dispersal rate can produce both an increase or decrease of the mean total population size.

The effect of dispersal on the fluctuation range largely depends on the intrinsic growth-rate parameters. Nevertheless, we can obtain some conclusions about how dispersal affects constancy and persistence. With regard to constancy, for relatively small values of r_B there is a significant interval of dispersal rates able to reduce the fluctuation range with respect to that of the isolated patches. Even more, we observe that a fixed point is stabilised in one case (panel G), so the total population size does not fluctuate. Panel G also shows a positive effect of dispersal on persistence since the minimum values of the total population sizes over the considered period of 100 generations are always greater than the correspondent minimum value

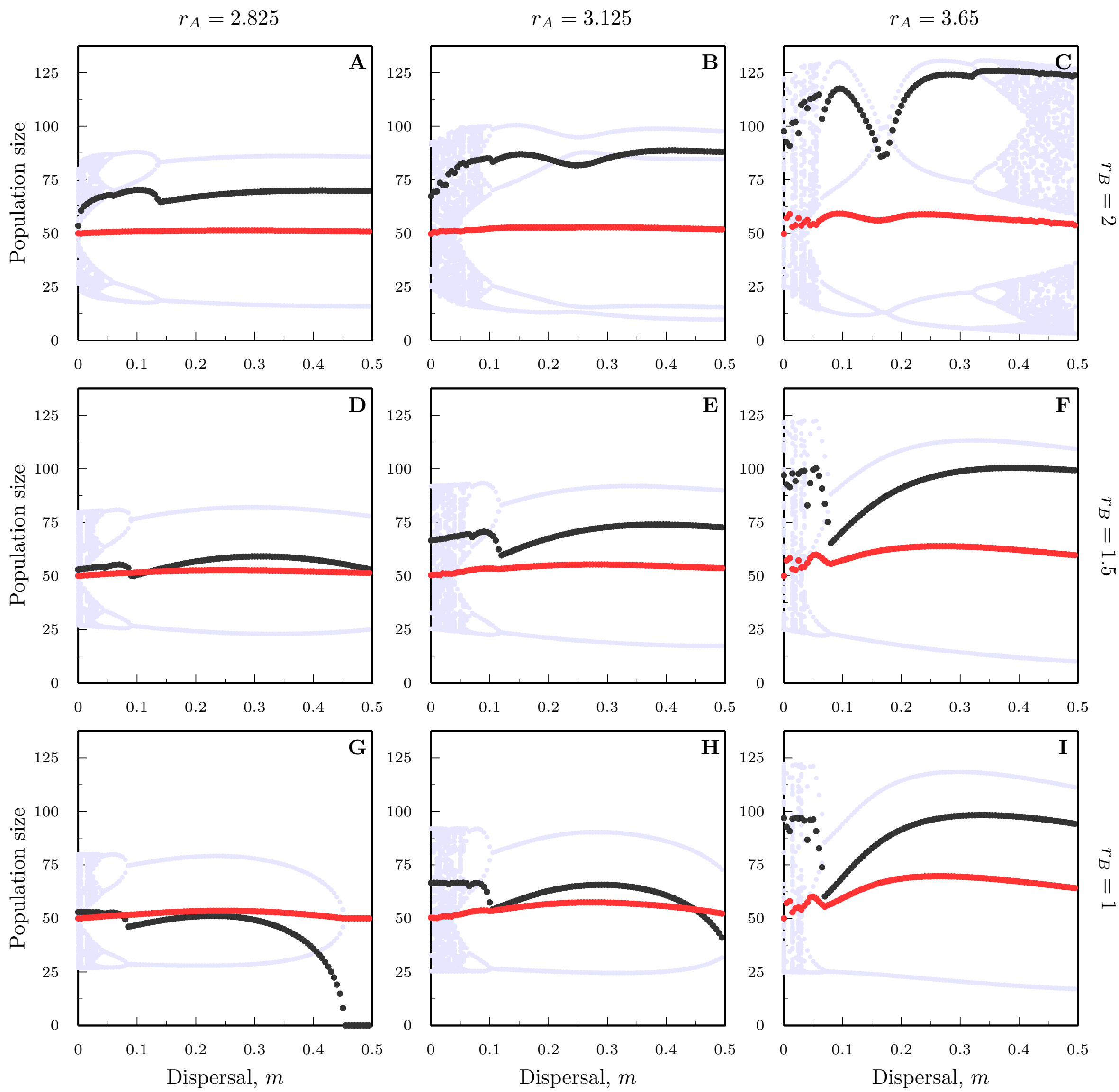

FIGURE 3. Bidirectional symmetric dispersal connecting a region with an attracting equilibrium to a region with complicated dynamics. The mean total population size (red) and its fluctuation range (black) overlie the bifurcation diagram, where the system was run for 3000 generations to remove transient effects, and then the total population size in the next 100 generations was plotted (light blue). See main text for a discussion of the results.

for unlinked regions ($m = 0$). But this does not happen for the rest of the cases, since those minimum values are larger than the minimum value for $m = 0$ for high dispersal rates only (panel H) or they are always smaller. Taking in consideration the mean total population size, persistence and constancy altogether, the situation that has a clearly better response to bidirectional symmetric dispersal than the others is the one with relatively small values of the intrinsic growth-rate of the subpopulations.

3.2. Effect of multistability

It is known that system (2.1) can exhibit multistability, i.e. the dynamics of the system depend on the initial population size [18, 24]. This occurs both for unidirectional and bidirectional dispersal. In this subsection, we address the question of whether or not multistability affects the behaviour of the mean total population size and its fluctuation range. We are particularly interested in how multistability affects their response to a variation of the migration rates. For this goal we use system (2.1) with parameters $r_A = 3.0$, $r_B = 4.0$, which leads to the coexistence of two different attractors both for unidirectional dispersal and bidirectional symmetric dispersal at certain dispersal rates.

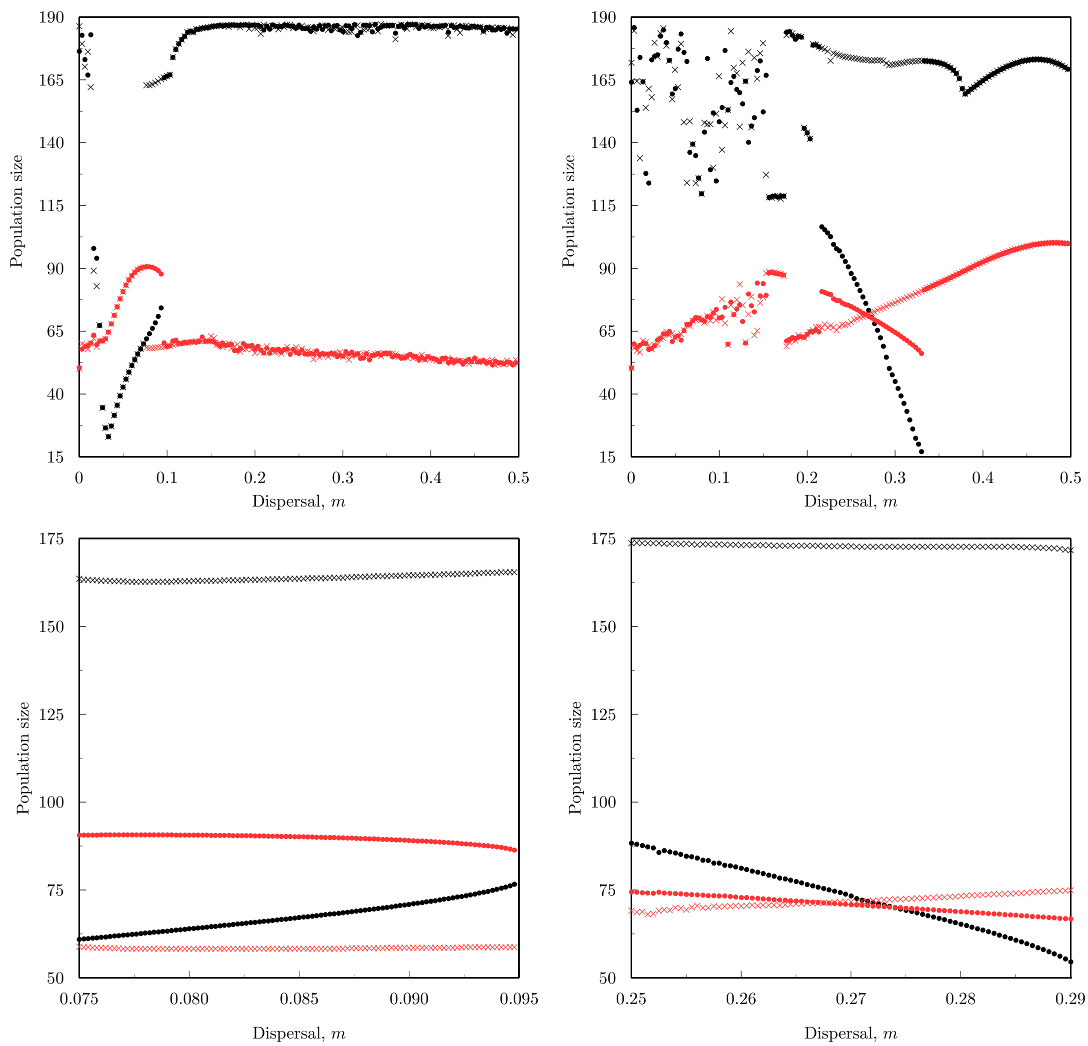

FIGURE 4. In each panel, the mean total population size appears in red and the fluctuation range is in black (both were calculated as in the previous cases). We use two different initial conditions, the crosses and filled circles correspond to each of them. In addition to the different responses to a variation of connectivity, note the differences in value depending on the attractor. Left panels show unidirectional dispersal, and right panels show bidirectional symmetric dispersal. Top panels show the behaviour for $m \in [0, 0.5]$, whereas bottom panels highlight specific subintervals of the parameter m. In all panels, $r_A = 3.0$ and $r_B = 4.0$.

Figure 4 illustrates that, depending on the initial condition, the mean total population size and its fluctuation range vary considerably. Further, increasing the migration has different consequences depending on the initial population size both for unidirectional and bidirectional dispersal. For instance, in case of bidirectional dispersal (right panels), the mean total population size decreases as m increases for one of the two considered initial conditions, but if we start with the other initial condition, then the mean total population size increases. Similar behaviours can be observed for the fluctuation range. Thus, the coexistence of alternative attractors seems to be a major problem from a control point of view, since depending on the initial condition a modification of migration rates to obtain certain effect could have the opposite one.

4. Summary

Many natural populations are formed by heterogeneous groups of semi-independent subpopulations connected by migration. The role of those connections in local and global dynamics is not completely understood. Our numerical study extends and complements existing investigations about the interaction between local subpopulation dynamics and dispersal that were focused on the complexity of the population dynamics [4]. Under a variety of dispersal scenarios and local dynamics configurations, we have considered the effect of dispersal on the mean total population size and on its fluctuation range. How dispersal affects these values (and consequently constancy and persistence) depends on the type of connection between subpopulations and the dynamics within them.

The main results of the paper are the following:

1. We find that the mean total population size of a spatially-separated population is clearly affected by the local dynamics and the type of connection involved. In most of the cases under consideration in this paper, the mean total population size of connected regions is greater than if those regions are isolated.
2. Both for symmetric bidirectional dispersal and for unidirectional dispersal from a donor with an attracting equilibrium to a recipient with complicated dynamics, the mean total population size generically has a unimodal response. But, for unidirectional dispersal from a donor with complicated dynamics to a recipient with an attracting equilibrium the response is monotone.
3. Connecting regions improves, in certain situations, constancy and persistence. But in other cases, this connection can have a negative effect on those characteristics.
4. We show that multistability affects the previous properties.

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References

[1] P. A. Abrams. *When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect.* Ecol. Lett., 12 (2009), 462–474.

[2] Y. Ben-Zion, G. Yaari, N. M. Shnerb. *Optimizing metapopulation sustainability through a checkerboard strategy.* PLoS Comput. Biol., 6 (2010), e1000643.

[3] R. Capeáns, J. Sabuco, M. A. Sanjuán. *When less is more: partial control to avoid extinction of predators in an ecological model.* Ecol. Complexity, 19 (2014), 1–8.

[4] S. Dey, B. Goswami, A. Joshi. *Effects of symmetric and asymmetric dispersal on the dynamics of heterogeneous metapopulations: Two-patch systems revisited.* J. Theoret. Biol., 345 (2014), 52–60.

[5] S. Dey, B. Goswami, A. Joshi. *A possible mechanism for the attainment of out-of-phase periodic dynamics in two chaotic subpopulations coupled at low dispersal rate.* J. Theoret. Biol., 367 (2015), 100–110.

[6] S. Dey, A. Joshi. *Stability via asynchrony in Drosophila metapopulations with low migration rates.* Science, 312 (2006), 434–436.

[7] M. Doebeli. *Dispersal and dynamics.* Theoret. Popul. Biol., 47 (1995), 82–106.

[8] D. J. Earn, S. A. Levin, P. Rohani. *Coherence and conservation.* Science, 290 (2000), 1360–1364.
[9] D. Franco, F. M. Hilker. *Adaptive limiter control of unimodal population maps.* J. Theoret. Biol., 337 (2013), 161–173.
[10] D. Franco, F. M. Hilker. *Stabilizing populations with adaptive limiters: prospects and fallacies.* SIAM J. Appl. Dyn. Syst., 13 (2014), 447–465.
[11] D. Franco, A. Ruiz-Herrera. *To connect or not to connect isolated patches.* J. Theoret. Biol., 370 (2015), 72–80.
[12] E. E. Goldberg, R. Lande. *Species' borders and dispersal barriers.* Am. Nat., 170 (2007), 297–304.
[13] A. Gonzalez, J. Lawton, F. Gilbert, T. Blackburn, I. Evans-Freke. *Metapopulation dynamics, abundance, and distribution in a microecosystem.* Science, 281 (1998), 2045–2047.
[14] N. J. Gotelli. *Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis.* Am. Nat., 138 (1991), 768–776.
[15] V. Grimm, C. Wissel. *Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion.* Oecologia, 109 (1997), 323–334.
[16] M. Gyllenberg, I. Hanski, T. Lindström. *A predator-prey model with optimal suppression of reproduction in the prey.* Math. Biosci., 134 (1996), 119–152.
[17] M. Gyllenberg, G. Söderbacka, S. Ericsson. *Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model.* Math. Biosci., 118 (1993), 25–49.
[18] A. Hastings. *Complex interactions between dispersal and dynamics: lessons from coupled logistic equations.* Ecology, 74 (1993), 1362–1372.
[19] A. Hastings, L. W. Botsford. *Persistence of spatial populations depends on returning home.* Proc. Natl. Acad. Sci. USA, 103 (2006), 6067–6072.
[20] F. M. Hilker, E. Liz. *Harvesting, census timing and "hidden" hydra effects.* Ecol. Complexity, 14 (2013), 95–107.
[21] A. R. Ives, S. T. Woody, E. V. Nordheim, C. Nelson, J. H. Andrews. *The synergistic effects of stochasticity and dispersal on population densities.* Am. Nat., 163 (2004), 375–387.
[22] D. Juher, V. Mañosa. *Spectral properties of the connectivity matrix and the SIS-epidemic threshold for mid-size metapopulations.* Math. Model. Nat. Phenom., 9 (2014), 108–120.
[23] B. E. Kendall, G. A. Fox. *Spatial structure, environmental heterogeneity, and population dynamics: analysis of the coupled logistic map.* Theoret. Popul. Biol., 54 (1998), 11–37.
[24] A. L. Lloyd. *The coupled logistic map: a simple model for the effects of spatial heterogeneity on population dynamics.* J. Theoret. Biol., 173 (1995), 217–230.
[25] R. Nathan. *The challenges of studying dispersal.* Trends Ecol. Evol., 16 (2001), 481–483.
[26] K. Parvinen. *Metapopulation dynamics and the evolution of sperm parasitism.* Math. Model. Nat. Phenom., 9 (2014), 124–137.
[27] W. E. Ricker. *Stock and recruitment.* J. Fish. Board Can., 11 (1954), 559–623.
[28] P. Sah, P. J. Salve, S. Dey. *Stabilizing biological populations and metapopulations through adaptive limiter control.* J. Theoret. Biol., 320 (2013), 113–123.
[29] J. Saldaña. *Modelling the spread of infectious diseases in complex metapopulations.* Math. Model. Nat. Phenom., 5 (2010), 22–37.
[30] R. V. Solé, J. G. Gamarra, M. Ginovart, D. López. *Controlling chaos in ecology: from deterministic to individual-based models.* Bull. Math. Biol., 61 (1999), 1187–1207.
[31] H. Thunberg. *Periodicity versus chaos in one-dimensional dynamics.* SIAM Review, 43 (2001), 3–30.
[32] J. E. Tillmann. *Habitat fragmentation and ecological networks in Europe.* GAIA-Ecological Perspectives for Science and Society, 14 (2005), 119–123.
[33] J. M. J. Travis, C. Dytham. *Habitat persistence, habitat availability and the evolution of dispersal.* Proc. R. Soc. B, 266 (1999), 723–728.
[34] S. Tung, A. Mishra, S. Dey. *A comparison of six methods for stabilizing population dynamics.* J. Theoret. Biol., 356 (2014), 163–173.