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Migration, coherence and persistence in a fragmented landscape

Yossi Ben-Zion · Yael Fried · Nadav M. Shnerb

Abstract The chance of local extinction is high during periods of small population size. Accordingly, a metapopulation made of local communities that support internal population cycling may face the threat of regional extinction if the local dynamics is coherent (synchronized). These systems achieve maximum sustainability at an intermediate level of migration that allows recolonization but prevents synchronization. Here we implement an individual-based simulation technique to examine the maximum persistence condition for a system of patch habitats connected by passive migration. The models discussed in this paper take into consideration realistic elements of metapopulations, such as migration cost, disordered spatial structure, frustration and environmental noise. It turns out that the state with maximum anti-correlation between neighboring patches is the most sustainable one, even in the presence of these complications. The results suggest, at least for small systems, a model independent conservation strategy: coherence between neighboring local communities has, in general, a negative impact, and population will benefit from intervention that increases anti-correlations.

Keywords Metapopulation · Coherence · Conservation

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Introduction

Growing concern over species extinction and the loss of biodiversity has led to many studies about the effects of habitat fragmentation on the sustainability of a spatially structured population (Fahrig 2003; Bascompte and Sole 1996; Kareiva 1987; Andren 1994; Debinski and Holt 2000; Keymer et al. 2000; Kruess and Tscharntke 1994; Pimm 1998; Lindenmayer and Fischer 2006; Earn et al. 2000). The extensive literature dealing with these topics has a very specific goal: developing the ability to predict the effect of an environmental change (urban development, new roads, climate shifts) on the persistence of species and eco-communities. Within this general framework, the concept of a metapopulation (Levins 1969) has received a lot of attention (Hanski 1999; Hanski and Gilpin 1991; Hanski and Ovaskainen 2000; Ricklefs and Miller 2000). In a metapopulation, the system survives due to recolonization of empty patch habitats by immigrants from other spatial patches. However, these turnover events are relatively infrequent, therefore the intra-patch processes must also be taken into consideration.

An analysis of ecological dynamics requires, beyond a good set of empirical measurements, a reliable conceptual framework within which the empirical studies can be analyzed and interpreted. A thorough understanding of the capabilities and shortcomings of the modeling technique is thus a crucial step towards rational planning of conservation policies. In particular, almost any real ecosystem (and even many experimental setups) admits highly complex structure (spatial, age) and is plagued by various types of noise [demographic, environmental (Bonsall and Hastings 2004; Matthies et al. 2004)]. Under these circumstances it is very hard

to deduce from the noisy data the exact dynamical law that governs abundance variation through time, so accessible models must neglect many of the features of the real system. Therefore, it would be desirable to identify the main factors that determine population sustainability by conducting a survey of many generic models under a wide range of realistic complications. To evaluate the chance of extinction, or to forecast the effect of human intervention, it is better to implement a scheme that does not depend on the features of any specific model, but rather takes into account the generic factors that affect population dynamics.

One of these factors is spatial coherence. Coherence, or synchronization among spatial patches (throughout this paper we refer only to zero-lag synchronization), is the case where abundance fluctuations are (positively) correlated among different colonies (Liebhold et al. 2004; Ranta et al. 1995). The primary mechanisms that synchronize abundance variation in different patch habitats are the movement of individuals between local populations and spatially correlated environmental fluctuations (the Moran effect).

Spatial coherence may facilitate extinction. A metapopulation survives local extinctions due to recolonization of empty patches by immigrants from nearby local communities. When the population of a species reaches its lowest level simultaneously in all habitat patches, there is a severe risk of regional extinction (Allen et al. 1993; Heino et al. 1997; Earn et al. 2000; Reichenbach et al. 2007). The importance of spatial coherence has been demonstrated in a wide variety of theoretical works dealing with periodic and chaotic dynamics of one species and victim-exploiter systems (Keeling et al. 2000; Abta et al. 2008; Seri and Shnerb 2010; Briggs and Hoopes 2004; Adler 1993; Abta et al. 2007; Ben-Zion et al. 2010b; Abbott 2011). Many experiments (Holyoak and Lawler 1996; Kerr et al. 2006; Dey and Joshi 2006; Molofsky and Ferdy 2005; Kerr et al. 2002; Vasseur and Fox 2009) also suggest that an increase in the migration rates may decrease the lifetime of the system as it induces spatial synchrony. On the other hand, some level of migration is necessary to keep the metapopulation alive, since it reduces the relative importance of abundance fluctuations and allows for recolonization of empty patches. The challenge is to find the optimal level of connectivity/migration and to suggest general guidelines for practical situations.

In a recent paper (Ben-Zion et al. 2010b) we have shown that the lifetime of the metapopulation under consideration peaked when the system reached a "checkerboard" state, i.e., when the correlations between neighboring sites were most *negative*. In this state, when the abundance in a certain habitat patch is low, its neighboring patches have large populations and thus the chance of recolonization is higher and the "buffering" against stochastic fluctuations is stronger.

This phenomenon involves two nontrivial effects. The first is the fact that migration may decrease the correlations, and even induce *anti-correlations*, between two neighboring patches. This counterintuitive behavior can be observed in panel (d) of Fig. 3 below: at low migration rates the correlation becomes more negative with the rate of movement. This has to do with the appearance of attractive orbits resulting from the deterministic dynamics (Kaneko 1990a, b; Kaneko and Tsuda 2000). Second, the local stability (Lyapunov exponent) of these attractive orbits has, in practice, nothing to do with the chance of extinctions. Since the system is subject to noise it eventually moves away from the linear stability region and preforms a long excursion in its way back to the attractive orbit. Extinction is plausible only during these long excursions (Ben-Zion et al. 2010b; Hastings and Wysham 2010). In the checkerboard state the local abundance at any instant takes an "up-down-up-down" state where migration from neighboring sites compensates for local fluctuations and the excursions are of relatively low amplitude.

The main goal of this work is to show that the results of (Ben-Zion et al. 2010b) hold when realistic complications are introduced into the simulations. Although we did not prove our results analytically, this numerical study covers many common scenarios that occur in metapopulation dynamics. For systems like those considered below (a small number of patches of similar size) we suggest, based on this work, a simple working principle: better persistence can be achieved by manipulating the system connectivity (or animal migration rate) such that the anti-correlations between neighboring patches becomes maximal. This maximum sustainability criteria may be implemented as a generic conservation strategy, which does not require the reliable identification of the underlying local dynamic. In the last section we will discuss some technical aspects related to the implementation of this maximum anti-correlation strategy.

To better understand the conditions under which the problem of coherence becomes important, let us consider a local community with a population dynamic that satisfies, up to demographic stochasticity, the Ricker map with nonoverlapping generations (Ricker 1954;

May and Oster 1976; Hastings 1996). In its fully deterministic version, the population at generation $t+1$ is related to the population in the former generation, N_t, by

$$N_{t+1} = N_t e^{r(1-N_t/N_0)} \qquad (1)$$

where N_0 sets the carrying capacity of the system, since above this density the population starts to decline. A metapopulation may be modeled by a collection of patches with the same parameters r and N_0, where the local map Eq. 1 alternates with passive diffusion movement among patches. A large area patch may be represented by a few units connected by strong migration.

In the parameter regime $r \leq 2$ the Ricker map admits an attractive fixed point, so the population density converges to some equilibrium value. In this case effects of coherence are small. For higher r, on the other hand, the population varies in time: a period-2 attractive orbit bifurcates into a period 4 and so on, until a fully chaotic orbit appears at $r = 2.6924...$. The chance of local extinction due to demographic fluctuations (the effect of environmental noise will be considered later on) is much larger when the population reaches its lowest level.

To find the chance for local extinction by demographic noise one should compare the infimum (lowest) value of N_t (for a given r, this number is determined by N_0) to the amplitude of demographic fluctuations. When these two numbers are of the same order of magnitude, extinction is plausible during the periods when the local abundance becomes small. When $\inf\{N_t\}$ is much larger than the fluctuation amplitude, local extinctions are rare, and the average extinction time grows exponentially with N_0 (Kessler and Shnerb 2007; Ovaskainen and Meerson 2010; Elgart and Kamenev 2004). If this is the case the possibility of regional extinction is negligible and the chance of exogenous catastrophes is probably larger than the likelihood of death attributable to the intrinsic dynamics.

Spatial coherence becomes an important factor when the local dynamics vary in time and N_t occasionally enters the dangerous zone where extinction due to stochastic fluctuations is plausible. We identify these types of systems as occasionally extinction prone: a local community from time to time reaches the extinction region owing to the variations induced by its intrinsic dynamics. When the local population is occasionally extinction prone, an isolated population goes extinct quite rapidly and metapopulation persistence depends on migration.

Many simple ecological models can describe an occasionally extinction prone system. First, all models that admit zero infimum (i.e., when the deterministic trajectory grazes the zero population state), such as the logistic map with $r=4$, the Nicholson-Bailey map (Nicholson and Bailey 1935) for host-parasitoid dynamics and the marginally stable Lotka-Volterra (Lotka 1920; Volterra 1931; Murray 1993) model with Holling's type I functional response (Holling 1965). Other models become extinction prone when the infimum population is small enough, e.g. the Ricker map for the N_0 values considered below, the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963) and the third case of the hawk-dove game considered by Durrett and Levin (Durrett and Levin 1994; Seri and Shnerb 2010). The class of occasionally extinction prone models does not include those used to describe extinction robust systems, for which the number of individuals is always large with respect to the size of the abundance fluctuations, or systems that support equilibrium density (like logistic growth with overlapping generations), where coherence has no role. For these systems an increase in the migration or the connectivity is always beneficial.

In (Ben-Zion et al. 2010b; Abta et al. 2007, 2008; Seri and Shnerb 2010) we considered many extinction prone models. Here, like in (Kessler and Shnerb 2010), we show results only for the Ricker system that allows for faster and easier simulations, but the results presented below have been verified for the other models mentioned above as well. As far as can be deduced from numerical experiments, it seems that the maximum anti-correlation strategy yields the longest persistence time for occasionally extinction-prone systems.

As explained above, the passage of individuals between spatial patches is crucial for the persistence of a metapopulation. When the extinction time of an isolated local community is larger than, or comparable to the time needed to recolonize an empty patch, there is no doubt: increased migration or increased connectivity are always beneficial (Durrett and Levin 1994; Barkham and Hance 1982; Snyder and Nisbet 2000). However, if the rate of migration is too strong it may induce spatial coherence in a finite system and expose the metapopulation to the danger of regional extinction. Accordingly, in occasionally extinction prone systems the dependence of the persistence time on the spatial connectivity, or the migration rate, is nonmonotonic. Practically, one can manipulate the connectivity by changing the topology of the system allowing more "corridors" between patches (Tewksbury et al. 2002;

Beier and Noss [1998](#); Gonzalez et al. [1998](#)), or by facilitating the passage of individuals. Sometimes there is an increase in the mortality of agents upon migration, a phenomenon we refer to as the migration *cost* (Motro [1982](#), [1983](#); Hamilton and May [1977](#); Taylor [1988](#)). This possibility is considered below.

For the class of dynamics discussed here, the optimal connectivity is an intermediate one: large enough to allow for recolonization events, yet not so large as to induce coherence. In the intermediate regime, local populations oscillate incoherently and local extinction is followed by recolonization as immigrants arrive from neighboring patches. Plotting the lifetime of the system vs. its connectivity results in a typical bell shape that peaks at intermediate connectivity. In (Ben-Zion et al. [2010b](#)) we showed that the lifetime peaked when the spatial pattern looked like a checkerboard, which is equivalent to maximum anti-correlations between neighboring patches. That paper dealt mainly with the abstract case of population dynamics on a lattice, i.e., where all habitat patches are the same and are organized in one- or two-dimensional arrays. Here we check the efficiency of the maximum anti-correlation strategy for more realistic scenarios (such as non bipartite spatial arrangements) and under other types of noise. We will show that it is indeed the maximum anti-correlation state (not necessarily in a checkerboard pattern) which is optimal in all the situations considered.

Before presenting the methods and the results we would like to clarify that the maximum anti-correlation strategy studied here is *not* evolutionary stable. In the absence of migration costs it is always beneficial to avoid kin competition by maximizing the dispersal distance or the migration rate. We have carried out numerical experiments of competition between two species with different migration rates and identical local dynamics. In all cases the species with the larger migration rate (or larger range of natal dispersal) wins, even when it leads to coherent variations and regional extinction. In models that explain the evolution of dispersal rates, such as the Hamilton-May model (Hamilton and May [1977](#); Comins et al. [1980](#)), the factors that balance the effect of kin competition are migration costs and local catastrophes, both affecting the average number of surviving offspring in the next timestep. Robustness against global effects, like coherence and regional extinction, cannot protect the population from invasion by mutants with a higher dispersal rate or range. Our results, thus, are relevant for the analysis of experiments and may be used to improve conservation strategies, but one should not expect natural systems in the wild to spontaneously take a checkerboard pattern.

Materials and methods

The time evolution of a population density described by a chaotic map like Eq. [1](#) cannot be solved analytically, and all the more so in the case of a coupled map where each map represents a single habitat patch, and the maps are coupled by migration. To get a reliable estimation of the system sustainability these deterministic equations could be integrated numerically over time, starting from typical initial conditions. However this method would involve picking an arbitrary threshold for extinction. So instead we chose to simulate the same dynamics with discrete individuals, i.e., to take demographic stochasticity into account by simulating the Ricker process with N_t that admits only integer values. This model is more appropriate for two reasons:

1. This method allows for a natural definition of (local and global) extinction: since the number of individuals is an integer, it may reach zero. (Other types of noise are considered below and are also simulated with individual-based dynamics.)
2. As explained by (Ben-Zion et al. [2010b](#); Kessler and Shnerb [2010](#)), a set of diffusively coupled chaotic maps may admit many attractive orbits with different periodicities. Once such an attractive orbit appears, one may guess that the system is not extinction prone anymore since the population never decreases below some minimum. However, in (Ben-Zion et al. [2010b](#); Kessler and Shnerb [2010](#)) we showed that some of these attractive orbits are not stable against noise such as demographic stochasticity. The erratic dynamics of a chaotic trajectory cannot be considered noise in that sense: nondeterministic noise should be added.

To simulate the discrete version of the Ricker map we have chosen r such that e^r is an integer (this somewhat simplifies the numerical procedure but it is not a necessary step). The map Eq. [1](#) is then interpreted as follows: on each island any agent produces exactly e^r offspring and dies. The chance of a given offspring to reach maturity depends on the number of competitors it has in the same patch and is given by $exp(-rN_t/N_0)$. The total population on the island at the end of the reproduction-competition step is a random integer taken from the binomial distribution $B(q, N)$, where the number of trials is $N = N_t exp(r)$ and the chance of success in one trial is $q = exp(-rN_t/N_0)$. The average number of individuals in the next generation, N_{t+1}, is given by $q \cdot N$, in agreement with Eq. [1](#).

After the reproduction-competition season comes the migration step, where any individual stays in its birthplace with probability $1 - \nu$ and decides to migrate

with probability v. The chance of an individual surviving the migration event is given by p; when $p = 1$ there is no migration cost.

In the large N_0 limit demographic noise is negligible and the dynamics obey the deterministic equation (Ben-Zion et al. 2010b; Kessler and Shnerb 2010) that describes the time evolution of a diffusively coupled chaotic map (Kaneko 1990a):

$$N_{t+1}^j = (1-v)N_t^j e^{r(1-N_t/N_0)} + pv \sum_i N_t^i . e^{r(1-N_t/N_0)} \quad (2)$$

The index i runs over all sites connected to the jth site. The goal of our numerical experiments is to identify the v_{opt} that maximizes the persistence of a system Eq. 2 to which demographic stochasticity has been added.

Results

Migration cost

The first case we would like to study is migration that has a cost. For a ring of four identical sites we have simulated the dynamics numerically as explained in the methods section. The local abundance N on a single habitat patch over time provides us with a time series. The first three panels of Fig. 1 show, for different values of cost p, an orbit diagram of the deterministic system obtained from numerical integration of Eq. (2). For each value of v the population N (of one arbitrarily chosen site) was marked on the corresponding vertical column.

As demonstrated by (Ben-Zion et al. 2010b), assessing the stability of these deterministic orbits using a
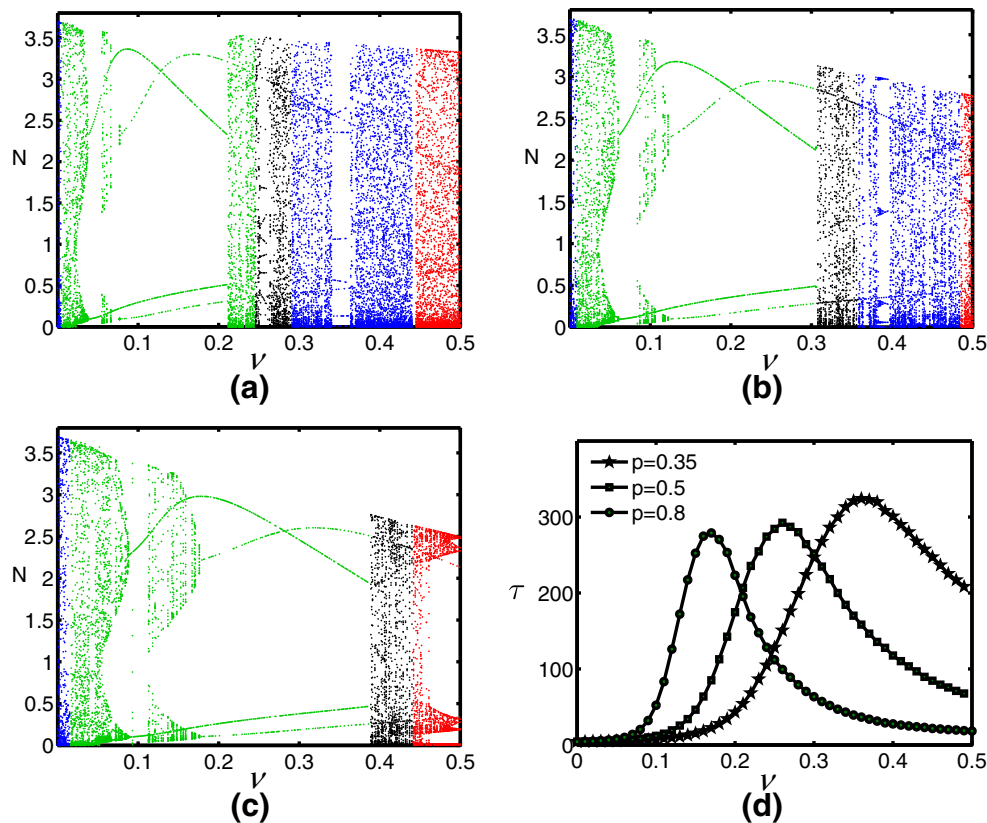

Fig. 1 A four-patch system of Ricker maps, coupled by density independent migration with periodic boundary conditions (ring). The chance of any individual leaving its location is v, and the probability of surviving the migration is p. The orbit diagram for the deterministic system with $r = 2.995$ is shown in the first three panels for different values of p. The region in the parameter space colored green is the values of v for which an up-down-up-down (UDUD - checkerboard) configuration appears. In this case local extinctions happen when the neighboring patches are densely populated. The black region corresponds to UUDD

spatial configurations. Red indicates full spatial synchronization. In the blue regions the local chaotic dynamics win and there is no spatial order; this may happen if migration is weak (the narrow blue area on the left) or in the transition region between two attractors. The survival probability (upon migration) is $p = 0.8$ $p = 0.5$ $p = 0.35$ for **a**, **b** and **c** respectively. Panel **d** shows the average time-to-extinction of the individual-based dynamics ($N_0 = 10$) for all three cases. The highest lifetime always appears in the UDUD region

local analysis technique such as the Lyapunov exponent may be misleading. The most important factor is the level of decoherence in the system, which is indicated here by the colors. Green indicates the anti-correlation region where the local increase of the population of a given site is followed by a local decrease in the neighboring sites (checkerboard). Since the actual system has four sites (each connected to two neighbors), the green is the "up-down-up-down" (UDUD) phase. Black indicates the region where an "up-up-down-down" (UUDD) phase appears. In the blue regions the dynamics are chaotic and in the red region all of the patches are synchronized (full coherence).

Panels (a–c) of Fig. 1 differ in a single parameter: the chance p of surviving a migration event. Panel (d) shows the average lifetime of the system in all three cases and demonstrates an important property: the optimal migration rate *grows* with the cost. Although migration becomes more "expensive", it pays for the system to increase the migration despite the cost. This result emphasizes the importance of maximum anti-correlation on the system's persistence, since as the checkerboard dynamics move to higher values, so does the ν_{opt}, causing the system to reach maximum sustainability at a higher migration rate. This phenomenon is further depicted in Fig. 2 for the whole $p - \nu$ space: ν_{opt} keeps an almost fixed distance from the right edge of the checkerboard region. Of course the maximum lifetime of the system, $\tau(\nu_{opt})$, decreases with the cost, as seen in Fig. 1d.
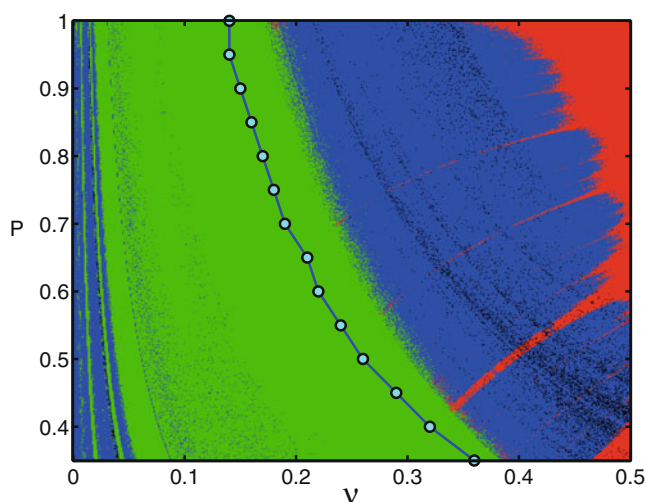
Figure 1 also demonstrates the *irrelevance* of what are perceived to be the stability features of the deterministic orbits. In Fig. 1a, for example, the system supports a stable orbit at $\nu = 0.2$, and a zero grazing chaotic trajectory at $\nu = 0.23$. However, there is no discontinuity, or any other pronounced effect, in the lifetime curve at Fig. 1d. Between $\nu = 0.3$ and 0.4 one observes another window of stability, but the lifetime decreases continually in this region: there is no benefit from entering the "stable" window. When the system was simulated with fluctuating migration rates, like ν alternating between 0.15 and 0.23 or 0.32, the lifetime obtained was some number between the lifetimes associated with the pure cases, again with smooth dependence and no discontinuities.

Complex spatial structure: the star network

Real metapopulations never occupy the vertices of a squared lattice. In most cases large and small habitat patches form some sort of scattered pattern in space, and a perfect checkerboard-like arrangement is not a realistic option. To check the effect of irregular spatial arrangement, two representative cases were chosen: the star network and an isosceles triangle. In both cases the spatial topology does not allow for bipartition.

The effect of connectivity on spatial synchrony has been investigated numerically by Holland and Hastings (2008), using deterministic Rosenzweig-Macarthur dynamics. They have found that the asymptotic state depends on the initial conditions, i.e., the system supports a few attractive manifolds, each with its own basin of attraction. In many cases they observed long transients before the system settled on the steady state. As shown in (Ben-Zion et al. 2010b; Hastings and Wysham 2010), the introduction of demographic noise allows the system to escape the deterministically attractive state and the main risk of extinction occurs during the transients, so the question of what happens when noise is superimposed on spatial irregular networks should be considered.

In (Ben-Zion et al. 2010b) we already examined a slight deviation from the bipartite lattice: a two dimensional array with a "defect", that is, one inaccessible habitat patch. It was shown that the system achieved maximum sustainability when the migration rate led to a checkerboard configuration swith some distortion close to the defect. Here we consider smaller systems where the spatial arrangement cannot be a checkerboard or an almost checkerboard, yet we will show that the robustness peaks when the spatial anticorrelations are as large as possible.

Fig. 2 The overall phase diagram for the 4-patch system. The colors indicate the different coherence regions as explained in Fig. 1 in the $p - \nu$ plan. The cyan dotted-line corresponds to the maximum lifetime obtained from individual-based simulations. Clearly, this maximum corresponds to the UDUD region of the deterministic map

The star network sometimes serves as a good proxy for a wide class of disordered networks (Ben-Zion et al. 2010a). The per-capita chance of migration is identical among all of the nodes, but they differ in the possible destinations for an emigrant: from an end node an individual must jump to the central site, but can choose among all of the end nodes if originating from the center.(see Fig. 3a).

Figure 3b presents the orbit-diagram of the (deterministic) star network. The parameter region where the central site is anticorrelated with the end nodes is colored green. In this region the individual-based simulation presented in Fig. 3c shows the life-time peak and (d) shows the anti-correlation between the central node and the average over all peripheral sites. Indeed, the maximum anti-correlation state is the more sustainable.

However, this system supports a secondary peak at much higher migration rates (see inset, panel c). This peak is not related to the appearance of a checkerboard, but instead is a result of the spatial heterogeneity. As explained in (Ben-Zion et al. 2010a), density independent migration within networks leads to accumulation of agents on the "hubs", i.e., on the sites with more links. This is a simple outcome of the laws governing migration in our model: every agent that leaves the end node must choose the center as its destination. When there are large differences between the populations on center and end nodes, the effective behavior of the system is as if there are different N_0s on the center and the peripheral nodes. The time it takes for a single "oscillation" (that is the time it takes the local population to reach high levels when starting from a low density, and decline back) depends on the population size. The system thus corresponds to local populations that oscillate with different periods and are coupled by migration. This scenario has been analyzed
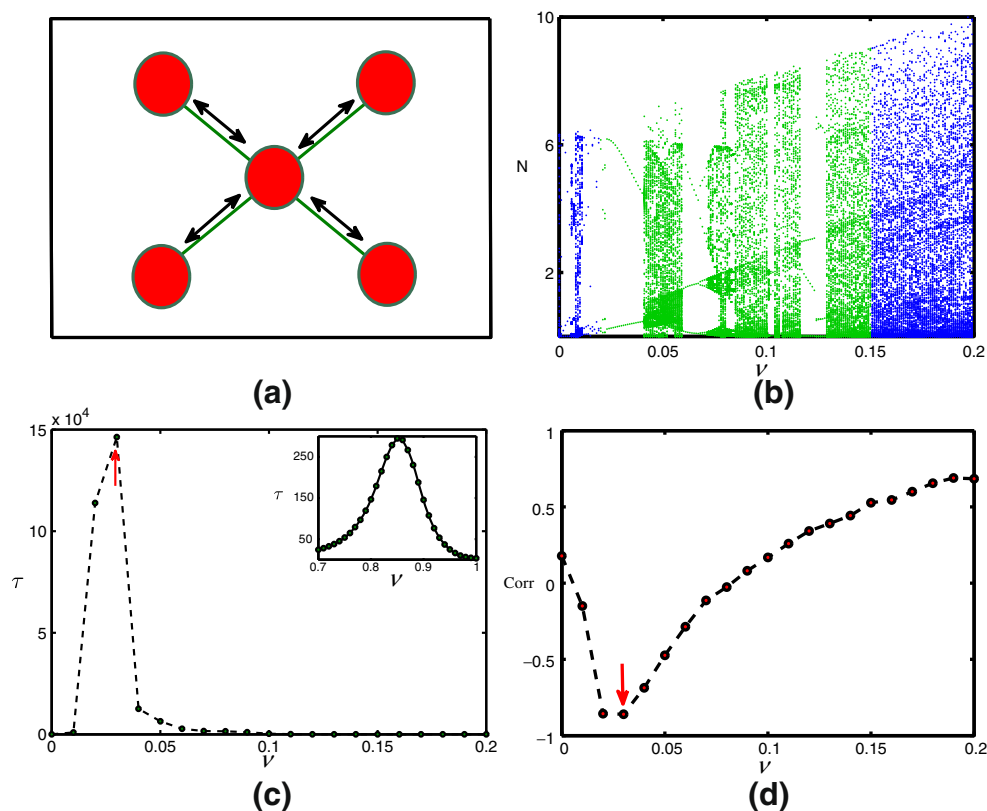

Fig. 3 The Ricker system on a star network appears in **a**. The orbit diagram for the deterministic system with $r = 4.304$ is shown in **b**. Here the maximum decoherence state (green) corresponds to an up-down spatial configuration, i.e., the population density on the central node is high, while the end nodes are almost empty and vice versa. The average time-to-extinction of the individual-based dynamics **c** peaked in the intermediate regime. The correlation coefficient between the central node and the average over all peripheral sites is shown in panel **d** the maximum decoherence state is indeed the most sustainable. The existence of another peak at high migration is emphasized in the inset of panel **c**. Unlike the low migration peak, the large peak is deterministic, i.e., corresponds to the appearance of stable orbits (negative Lyapunov exponents) in the bifurcation diagram, for $N_0 = 10$

in (Yaari et al. 2008), and was shown to support stable orbits even without demographic noise. Unlike the low-migration peak, the location of this sustainability point at high migration may be inferred from an analysis of the linear stability of the deterministic orbits.

A second case of a small disordered array is the isosceles triangle, the results of which are depicted in Fig. 4. Here we investigated a range of scenarios, from the case where patches 1 and 2 are closer (there is more movement between them) while patch 3 is more isolated, to the opposite situation where the distance between 1 and 2 is large. In all cases, the probability of an individual leaving site 1 (or 2) is $\nu + \nu_0/2$, while the chance of leaving 3 is ν_0. An emigrant from 3 jumps to 1 or 2 with equal probability, but an individual that leaves 1 (2) moves to 2 (1) with a chance $1 - \mu$ and to 3 with a chance μ. The parameter μ is not arbitrary: $\mu \equiv \nu_0/[2(\nu + \nu_0/2)]$. With that, the flow of individuals along the links $1 \leftrightarrow 3$ and $2 \leftrightarrow 3$ if equal and symmetric, with $\nu_0/2$ immigrant on average, and the link $1 \leftrightarrow 2$ is also symmetric with migration rate proportional to ν. By varying ν we can control the proximity of 1 and 2: the case $\nu = \nu_0/2$ corresponds to a equilateral triangle, if $nu = 0$ there is no direct transfer of individuals between 1 and 2 ($1 \leftrightarrow 3 \leftrightarrow 2$) and for large ν the 1–2 link is much stronger than 1–3 and 2–3.

Figure 4 shows that, when varying the migration between 1 and 2, maximum sustainability appears when the anticorrelation between 1 and 2 peaks, independent of the correlations with 3. Thus it seems that for small

scattered arrays one can manipulate the connection between two habitat patches to achieve anti-correlation and this will increase the lifetime of the system, no matter what the state of the other patches is.

Frustration and semi-checkerboards

In condensed matter physics many systems attain their minimal energy when their spatial arrangement is checkerboard-like. A classic example of this is a lattice occupied by small magnets for which in the low energy state every "up" spin is surrounded by "down" spins (antiferromagnetism). The low-energy state may take this checkerboard configuration, of course, only on a bipartite lattice. The behavior of these systems on non-bipartite arrays, like the two dimensional triangular lattice, is much more complicated.

The term used to describe the problem of optimal arrangement on a non-bipartite lattice is *frustration* (Thouless et al. 1977). The simplest example is a triangle: one cannot have a perfect up-down-up-down arrangement on a triangle: one link, at least, must be frustrated. In this section we show the results of our simulations when carried out with a frustrated arrangement of spatial patches. Two generic examples have been studied: the triangle and the pyramid (a four-patch system of fully-connected sites).

Both perfectly ordered bipartite lattices and fully frustrated systems are rare in nature. They are considered here because they appear often in experimental setups, and because they present two extreme cases which allow the classification of realistic patterns according to their proximity to one of these extremes.

The dynamics of the deterministic three-patch system of coupled Ricker maps is depicted in Fig. 5a. The graph shows three different behaviors: in the case of low migration the system behaves as a collection of independent chaotic patches (blue region), at high migration the whole system synchronizes (red region) and at an intermediate migration rate (green) the system presents a *semi-checkerboard*: two patches synchronize and oscillate in phase with the other patch. This feature is demonstrated in Fig. 5d, showing the correlation coefficient between different patches. In the semi-checkerboard region the individual-based simulation presented in Fig. 5b shows the maximal life-time. Panel (c) presents the Lyapunov exponent λ of the orbits: while the chaotic regions are characterized by a positive exponent indicating that the trajectories are unstable, for the periodic orbits λ is negative. However, although there are more attractive (more negative λ) regions, the lifetime peaks [panel (b)] when the decoherence is maximal.
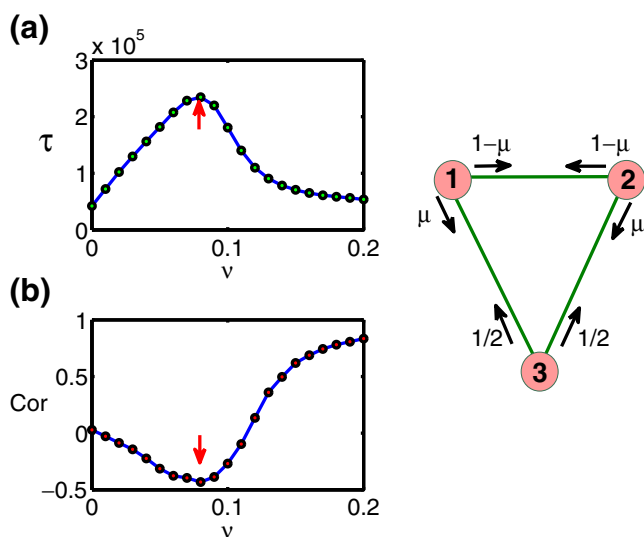

Fig. 4 A triangular setup (see sketch, right panel). When the migration rate between 1 and 2, ν, varies, the maximum sustainability appears when the correlations between 1 and 2 (lower panel, left) are most negative
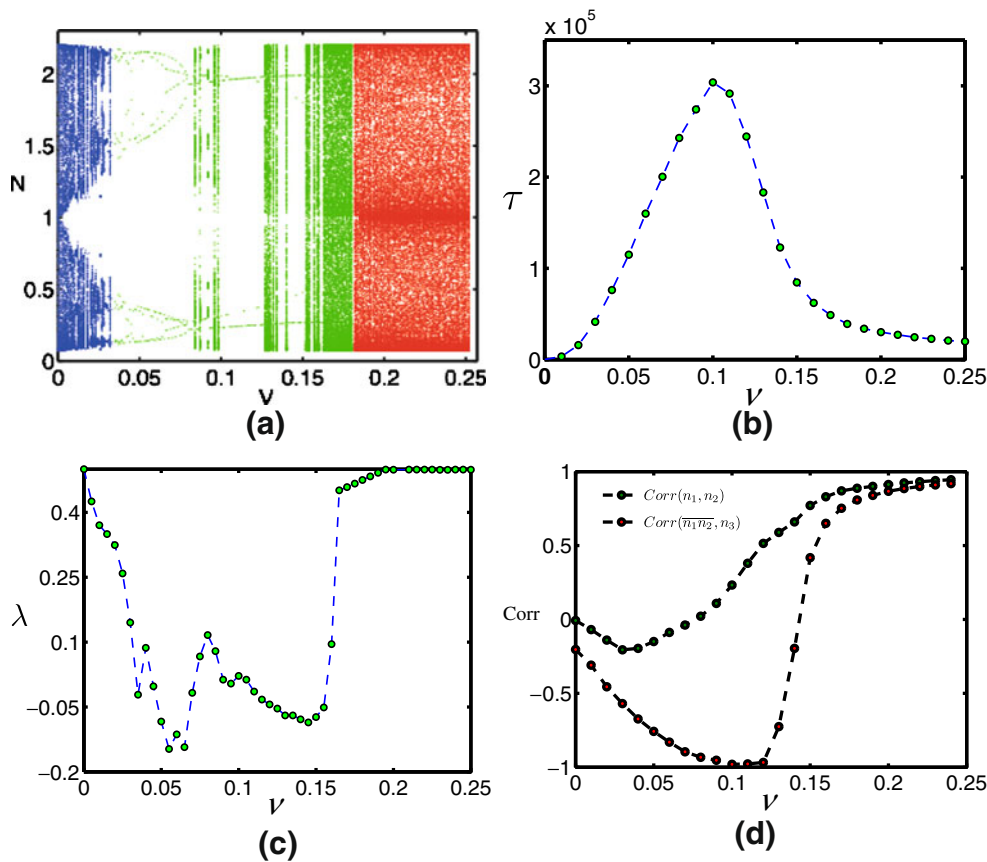
Fig. 5 A three-patch system of coupled Ricker maps. **a** The orbit diagram for the deterministic system with $r = 2.833$. The intermediate migration (green) regime is characterized by a frustrated spatial configuration; two patches are locked together and their oscillations are anticorrelated with the third. Initial conditions break the symmetry among patches. The average time-to-extinction of the individual-based dynamics of the same system is plotted in **b**. The highest lifetime correspond to the up-down region of the deterministic map, for $N_0 = 30$. **c** shows the Lyapunov exponent λ of the orbit: while the chaotic regions are character-ized by a positive exponent indicating that the trajectories are unstable, for the periodic orbits λ is negative. Yet, although there are more attractive (more negative λ) regions, the lifetime peaks when the decoherence is maximal. This is emphasized in panel **d**, where the correlation coefficient between patches is plotted. Here the green points correspond to the correlations between the two synchronized patches, while the red shows the correlations between the average of the two synchronized patches, $n_1^- n_2$, and the third patch

The *semi-checkerboard* pattern also characterizes the maximum sustainability point of the pyramid (Fig. 6), a fully connected four patch system. In this case the system spontaneously divides itself into two synchronized parts presenting up-down dynamics in intermediate diffusion.

Another issue addressed in Fig. 6 is the effect of connectivity. The main part of Fig. 6b shows the lifetime of a four-patch system in a fully connected configuration (any immigrant chooses one out of three patches with the same probability) and the inset shows the lifetime of a four patch system on a ring, i.e., when the passage of individuals is to neighboring patches only. In both cases ν determines the chance of migration per individual, which is independent of the connectivity of the system. The lifetime peak appears to be at a very similar migration rate, but its height is smaller (by a factor of 10) for the fully connected system, i.e., an increase in the connectivity decreases the average lifetime.

Environmental noise

In the previous sections only one type of noise, demographic stochasticity, was considered. The importance of including this type of noise is that it allows for a natural definition of the extinction as the inactive ("absorbing") state of zero population, and that it exists even in controlled experiments. It is well known, however, that other types of noise affect realistic eco-communities. In (Ben-Zion et al. 2010b) we examined
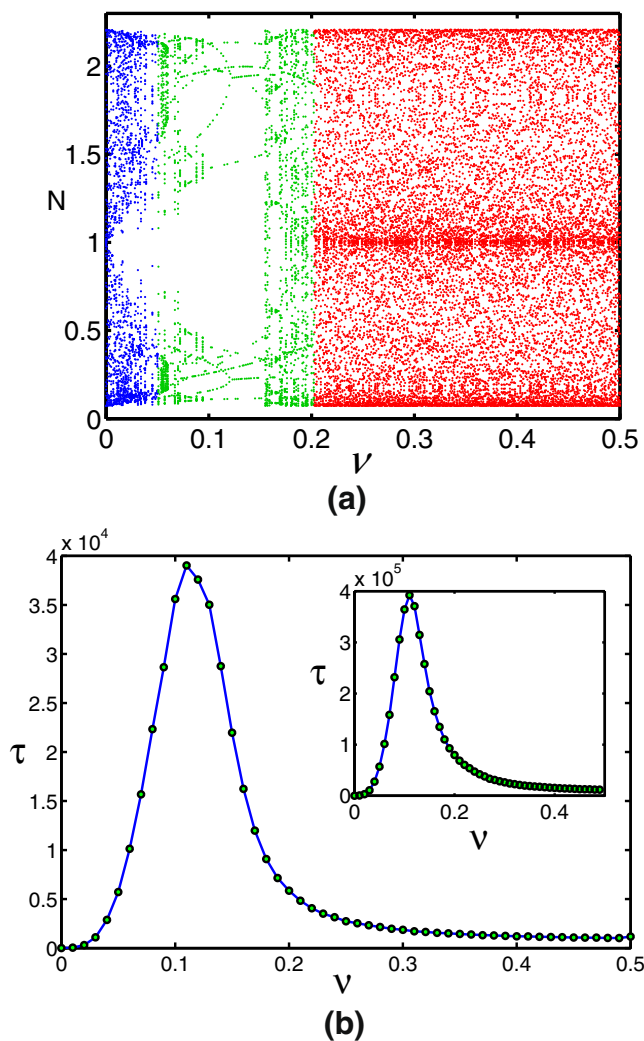
Fig. 6 A four-patch system of fully-connected coupled Ricker maps. **a** The orbit diagram for the deterministic system with $r = 2.833$. In the low-migration (blue) region the patches are independent, while in the high migration (red) region they are synchronized. The intermediate migration (green) regime is characterized by two coupled synchronized patches that behave with UD dynamics. **b** shows the average time-to-extinction of the individual-based dynamics of the same system. The highest life-time corresponds to the up-down region of the deterministic map, for $N_0 = 20$. The inset shows the same for a four-patch system on a ring, i.e., with decreased connectivity (the same topology as the one used in Fig. 1). While the peak appears at a similar migration rate, its height is an order of magnitude higher

and Kaitala 2006) we simulated this map, and added stochasticity ξ

$$x_1^{t+1} = \xi_1 \left[(1 - \nu)x_1^t e^{(r(1 - x_1^t/N_0))} + \nu x_2^t e^{(r(1 - x_2^t/N_0))} \right]$$

$$x_2^{t+1} = \xi_2 \left[(1 - \nu)x_2^t e^{(r(1 - x_2^t/N_0))} + \nu x_1^t e^{(r(1 - x_1^t/N_0))} \right]. \quad (3)$$

The noise terms ξ are uniformly distributed random numbers in the range between $1 - w$ and $1 + w$, where $w = 0.2$.

Equation 3 describe a system with no demographic stochasticity, where the size of the population may take noninteger values. At the end of each time step, Eq. 3 yield two numbers, x_1 and x_2, which are the expected average population on the corresponding islands. To make this model individual-based the following procedure has been adopted: at each time step two integers, n_1 and n_2, were drawn at random from a Poissonian distribution with an average of x_1 and x_2; these integers were then fed back as the population size for the next iteration of Eq. 3.

We simulated the system and measured the persistence time as a function of the the migration rate for two different noise terms: perfectly correlated stochasticity and stochasticity with no correlation at all (Ranta
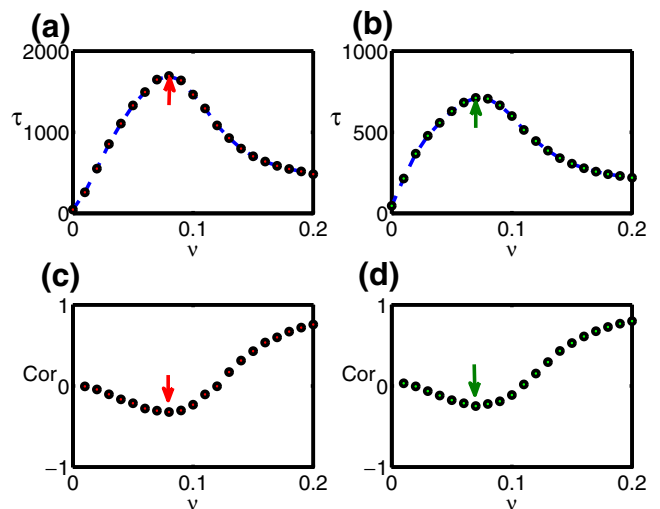

Fig. 7 The average persistence time of a two-patch system with uncorrrelated (left) and correlated (right) dichotomous environmental noise. The intra-patch dynamics follows the Ricker map with $r = 2.83$ and N_0 is chosen randomly as either 30 or 36. Panels **a** and **c** show the average time to extinction and the correlation coefficient, correspondingly, for simulations where the value of N_0 was picked at random for each of the patches independently. Panels **b** and **d** show the same for correlated environmental noise where the same N_0 is chosen at each generation for both patches. The lifetime of the Moran system is shorter and the peak is shifted to smaller migration rates, but both peaks appear where the decoherence is maximal

the impact of other types of noise and the robustness of the checkerboard strategy. For the sake of completeness we review the main results here. We also present another numerical experiment that demonstrates the effect of synchronous exogenous factors [the Moran effect Moran (1953)]

In (Ben-Zion et al. 2010b) we considered a two-patch Ricker system, and following (Ranta et al. 2006; Ranta

et al. 2006; Ripa and Lundberg 1996). The results, presented in (Ben-Zion et al. 2010b), show that in both cases the sustainability peaks at the same ν for which the maximum anti-correlation appears for the case of pure demographic noise. The overall life-time is smaller in the presence of environmental noise as expected.

In all of the examples presented so far, spatial synchrony was a result of dispersal. However, positive correlation may arise as a result of congruent dependence of population size on exogenous random factors (Liebhold et al. 2004; Moran 1953; Sutcliffe et al. 1997). What happens to the sustainability peak in that case?

In Fig. 7, the lifetime of a two-patch system with dichotomous noise is presented together with the correlation function. If noise is uncorrelated between patches the persistence peaks (panel a) when the coherence is minimal (panel c). When the environmental noise is correlated (left panels b and d) the point of maximum decoherence moves to lower migration rates, and so does the maximum lifetime.

Discussion and conclusions

Theoretical studies emphasize the contradictory influences of dispersal on the sustainability of animal colonies. On the one hand, systems with a low rate of dispersals cannot survive, but on the other hand large migration leads to coherence and exposes the system to the danger of regional extinction. This observation is supported by recent experiments. In (Dey and Joshi 2006), for example, laboratory metapopulations of Drosophila under different migration rates were replicated. The experiment presented maximal sustainability in an intermediate dispersal rate; the optimal rate appears when the system presents anti-correlation among neighboring subpopulations. The achievement of ecological sustainability in intermediate diffusion has been demonstrated in other recent experiments on predator-prey (Holyoak and Lawler 1996; Ellner et al. 2001; Kneitel and Miller 2003; Kerr et al. 2002), host-parasite (Kerr et al. 2006) and single species (Molofsky and Ferdy 2005) colonies.

In our previous study (Ben-Zion et al. 2010b) we found that the optimal strategy is an intermediate level of dispersal that manifests itself in spatial checkerboard patterns. This structure facilitates movements between colonies that are in opposite states at a given time. In this study we have examined the performance of this strategy when some realistic aspects are added to the model and when the spatial structure does not allow for a checkerboard pattern. We considered the stability in the presence of migration cost, and showed that as the lifetime peak moves to the right (higher migration), so does the maximum anti-correlation state. Correlated environmental noise shifts the peak to a lower ν, and again the maximum decoherence state moves accordingly. The same holds true for different topologies. It turns out that in all cases, maximum sustainability is achieved where the anti-correlations between neighboring subpopulations reach the highest value.

The checkerboard strategy, as emphasized above, is not evolutionary stable, and is not expected to appear spontaneously in nature. (It is interesting to note, though, that the results of Matter and Roland (2010) may be interpreted as the destruction of an existing checkerboard pattern due to local extinction.) The result presented here may be useful for the interpretation and planning of experiments with spatially structured populations (from single species to microcosms) and for the management of conservation efforts, especially those that involve manipulation of connectivity and migration rates. The main recommendation is very simple: in the interesting parameter regime, i.e., when an isolated population is occasionally extinction prone, the persistence of the system depends, almost solely, on the level of coherence among patches. The conservation strategy has to rely on this observation, and any intervention should be aimed at making the anti-correlations as high as possible.

In most practical cases, an accurate retrieval of the "laws of motion" that govern the local population dynamics is almost impossible. The strong effects of noise and migration make this task hard even in the simplest experimental situations [see, for example, the level of noise presented in the recurrence plots used in Molofsky and Ferdy (2005)], not to mention in the results obtained from field studies. One would like to have a model-independent tool that allows the prediction of the outcome of a manipulation. This work seems to suggest a generic rule of thumb: try to maximize the spatial anti-coherence. This strategy works for all of the cases we have studied here, which together provide a fairly comprehensive survey of small systems with similar-sized patches.

When pairs of patches were already anti-correlated, we have not yet found a reliable way to decide if the system is to the left of the peak or to its right (will the anticorrelation/lifetime increase or decrease when the migration rate becomes larger/smaller), but in the meantime, a trial and error strategy can be used. However, when two nearby local communities show synchronous population dynamics [i.e., when the zero-

lag correlation between population sizes is positive, like in the microcosm experiment of (Holyoak and Lawler 1996)] a decrease in the connectivity/migration between them is always beneficial for the sustainability of the system, no matter what the underlying dynamics are.

Finally, let us comment about one of the techniques developed by ecologists in order to predict the danger of metapopulation extinction, which is based on the stochastic patch occupancy models (SPOMs) (Moilanen 1999; Etienne et al. 2004; Hanski 1994a, b, 1991; Moilanen 2004). These models treat spatial patches as a two-state system, where each habitat patch is either occupied or empty. The underlying assumption is that the timescale in which the population reaches its local carrying capacity is relatively small. Neglecting the details of the intra-patch dynamics, the theory focuses on extinction and recolonization events. Most importantly, decoherence among local habitats is implicitly *assumed* in this model since it postulates that the chance of local extinction decreases monotonically with the connectivity. The simulations presented here show that, by assuming decoherence, the analysis suggested by SPOM may miss the most important stabilizing factor, at least when the local abundance is occasionally extinction prone. In a different publication, we intend to explore the parameter regime where SPOM is applicable, and to explain how to use the presence/absence data in order to check if the system is indeed within this parameter regime.

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