Coherence, conservation and patch-occupancy analysis.

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Abstract:

Spatial coherence (synchrony) among subpopulations poses a danger to the metacommunity, as it increases the risk of regional extinction. When this effect is significant, the use of inference technique based on the stochastic patch occupancy model (SPOM) may be inadequate, since SPOMs assume that each habitat patch is either occupied or empty and neglect the intra-patch dynamics. Here we suggest a general classification of the dynamics that allows one to identify, in a model-independent way, the regimes where coherence effects are strong. We also present a new technique, based on patch occupancy (presence/absence) data, to identify the role of spatial coherence in the stabilization of a metapopulation and to give an early warning against the possibility of regional-scale extinction. When this scenario occurs a *decrease* in the movement of individuals (habitat fragmentation, reduced dispersal rates) has a positive effect on the sustainability of the spatially distributed population. The results of individual based simulations of a spatially structured population are analyzed with SPOM and the regime where the two-state approximation is fails is identified.

Introduction

One of the main challenges in the practice of ecologists is to assess the risk of extinction of a spatially structured population of certain species. In many cases, the movement among subpopulations is affected by human activities that alter natural migration patterns by changing the connectivity (habitat fragmentation, conservation corridors (*1*)) or the dispersal rates of individuals. Prior knowledge about the dynamics of such a system is generally very limited, as the time series collected for the spatio-temporal abundance of local populations, if any, are typically solitary, poor, noisy and short. Accordingly, one would like to implement some generic algorithm that does not depend on any specific detail of the population dynamics with gross parameters that can be estimated even from crude datasets, like those showing only presence-absence of individuals on a habitat patch.

One popular technique of this kind is based on the stochastic patch occupancy model, SPOM (*2-5*). This model assumes that each patch is either empty or posses more or less its carrying capacity, i.e., it allows only two states for each subpopulation. Then it assumes that the chance of local extinction decreases and the chance of recolonization increases, with the number of occupied neighboring patches. Under these assumptions, an increase in the connectivity or the dispersal rate always increases the lifetime of the population, so the prediction that conservation corridors will enhance sustainability is not an outcome of the model but part of its assumptions. SPOM-based algorithms only quantifies how much gain one gets from a certain manipulation that facilitates movement, but the qualitative effect is presupposed.

There is a regime where this outlook, and the SPOM algorithms, is very efficient. Increasing the connectivity between habitat patches or islands allows for recolonization, decreases fluctuations and, accordingly, is considered in general as a stabilizing factor (*6-9*). There are, however, scenarios where an increase in the connectivity, or in the movement of individual inhabitants, induces coherence (synchrony) among patches and increases the risk of regional extinction. In this regime, movement and connectivity *reduce* the sustainability of the system (*10, 11*).

The negative effect of coherence among subpopulations on the sustainability of spatially segregated systems has been confirmed in a series of laboratory experiments (*12-18*), and is the subject of many recent theoretical works (*19-21*). Less attention has been devoted to the observation of this effect in field studies: when the analysis is carried out using SPOM one cannot detect this phenomenon since SPOM neglects the intra-patch dynamics as will be discussed in detail below. One would like, thus, to have a diagnostic tool that allows for the detection of coherence effect given a low-quality timeseries. In almost all practical cases the data collected does not allow the researcher to identify the exact model that describes the population dynamics, not to mention a retrieval of the model parameters.

The aim of this paper is to provide such a tool. To do that, we are following a few steps:

1. In sections 1 and 2 we are trying to identify the parameter regimes where the effect of coherence is significant (and SPOM may become inadequate) by looking at a few standard models of population dynamics. The goal of this discussion to provide a qualitative insight: coherence is relevant when the subpopulation dynamics is time-varying and extinction-prone. These crude features, although extracted from theoretical analysis of models, are generic and model-independent, and one may be able to identify them even using short-time noisy data.

2. In section 5 we present a technical tool that utilizes presence/absence data and provides quantitative measure for the effects of coherence. This is done, basically, by showing deviations from the predictions of SPOM. To do that we first analyze the assumption of SPOM in detail (section 3) and present an individual-based simulation procedure that imitates a realistic system and allows for a comparison between the stabilizing and the destabilizing effects of migration (section 4).

It should be noted that spatial synchrony is not the only factor that limits the stabilizing effect of dispersal. In some ecosystems there is a "cost" for migration, e.g., an increased mortality of individuals that leave their habitat (*22-24*). Increased movement among patches leads, in these systems, to a higher death rate and extinction. We are not dealing with this effect here. Changing the connectivity of the spatial network by introduction of conservation corridors may also by problematic if it allows for invasion by exotic species, movement of overzealot predators between patches and the spread of infectious diseases (*25, 26*). We are not dealing with these effects here.

To start, let us remind the known facts about the role of migration in spatial ecological communities and provide more introductory material.

A metapopulation is made of many distinct subpopulations connected by migration. Here we consider only density independent (passive) migration, so the chance of emigration and the success of recruitment do not depend on the local population density. An increase in the level of migration (either by changing the connectivity of the system, e.g., by the construction of corridors, or by manipulations of the level of individual's movement) leads to the reduction of spatial variance. This has two outcomes:

1. When the transfer of individuals among patches is frequent one may consider a few nearby patches as if they were effectively a single habitat. The size of the population on this effective patch is the sum of the local populations. Accordingly, the relative importance of demographic or (spatially uncorrelated) environmental fluctuations decreases. This size effect by itself is a stabilizing factor, as it "*buffers*" the population from stochastic variations and decreases the risk of extinction as the relative amplitude of fluctuations (compared to the total size) declines (*27, 28*). Migration also facilitates the recolonization of empty patch habitat (rescue). Along this paper we refer to all these effects – the stabilizing aspects of migration – collectively as the "buffering effect".

2. Migration acts against spatial variations and leads to more *coherence (synchrony)* among local patch habitats. This effect is potentially dangerous, as it may expose the population to the threat of regional extinction, when all local habitats reach the low-population state at the same time.

In the relevant parameter regime the buffering effect and the increase of coherence may interfere, and one would like to know which of them is stronger. It turns out that the answer depends very much on the local dynamics of the system, which may be extinction robust or extinction prone. In the next section we explain these terms, show that the buffering effect of population size depends strongly on these features and that for extinction prone dynamics the benefit from an increase of the population size is quite limited. In section 2 we show under what conditions spatial coherence poses an important threat to persistence and increased connectivity becomes dangerous. In this parameter regime, it is important to obtain a measure of the ratio between these effects in order to predict, or at least to suggest an educated guess about, the results of habitat fragmentation or an increase in the connectivity.

Popular inference tools for field data, like SPOMSIM (*2*), are based on the stochastic patch occupancy model. In the third section we explain why this method cannot detect coherence or its absence. This has to do with the projection of all intra-patch states on a single state ("occupied") implemented by SPOM. Individual based models, like the one presented in section 4, allow one to estimate the importance of both buffering and coherence effects, but it is quite difficult to infer their parameters from field observations. In the last section we suggest a method that, like SPOM, utilizes presence/absence data only, but allows one to detect that the system is actually at the range of parameters where spatial coherence is an important destabilizing factor. This method may be used in order to identify the coherence effects in field data and, more practically, to find out when increased connectivity becomes harmful; in this parameter regime a reduction in the number of links, rather than the construction of conservation corridors, is the recommended conservation strategy.

Throughout this paper we are deliberately switching between different models of population dynamics. Clearly, all models of ecological communities are approximations, and one would like to find generic insights, rather than model-specific results. Our goal here is to study some common features of all these models in order to achieve generic qualitative insights and to develop ability to detect different regimes. Although we cannot suggest an algorithm that predicts extinction times from the available data, we can provide a few rules of thumb that may assist conservation management. In particular, the technique suggested here may detect where, in a spatially extended system, the population suffers from overcoherence; in this spatial region one would like the decrease the movement of individuals and to avoid conservation corridors.

1. *Extinction prone vs. extinction robust dynamics and the importance of population size.*

The basic distinction we are making in this section is between stable and extinction prone systems. To get some intuition, let us take a look at Figure 0. Four hypothetical timeseries describing the abundance of local population are presented. These timeseries were generated using standard population dynamics models with noise. By smearing the data one can distinguish between the average trend associated with the deterministic model (the full line) and the erratic jumps associated with the stochasticity. A system is extinction prone if these random fluctuations may drive it to extinction, i.e., if the "width" of the line in its lowest points (the infimum) is touching zero.

Another important distinction we would like to make is between systems (like the Malthus-Verhulst logistic growth discussed below) that support an equilibrium population and time varying systems. For an equilibrium dynamics the stochastic fluctuations are spread around a fixed value, as demonstrated by the two upper panels of Figure 0, where the line that represent some moving average stays almost fixed after a short period of equilibration, and extinction occurs due to large fluctuations (see also Fig. 4). Other population dynamics systems support internally driven population cycling so the average population density is oscillating in time. As we shell show below, for spatially distributed population coherence effect are much more pronounced when the system is time-varying.

The rest of this section is devoted to a more detailed analysis of the conditions for "extinction proneness" in technical terms associated with specific models and a few types of noise, but the overall picture is model independent so the uninterested reader can skip the discussion below and move to the last paragraph of this section.

We are implementing here a few elementary (single and two species) population dynamics models that are widely used in the analysis of simple eco-communities (*29*). These models (like logistic growth, Nicholson-Bailey model for parasitism and so on) are all deterministic and lack of any spatial structure (well-mixed population). Moreover, the population density in these models never crosses zero, i.e., the model *per se* does not allow for extinction (*30*).

To assess the chance of extinction one should add a threshold for the dynamics, assuming that if the population is below some level it effectively perished. If extinction happens due to stochastic events (a few bad years, accidental death of animals) noise must be added to the model. One of the most important forms of noise is demographic stochasticity (*31, 32*), which is inherent to any population dynamic. This noise yields fluctuations in the population size and allows for a natural definition of the extinction state as the case where the population reaches zero (an absorbing state), so there is no need to introduce an artificial threshold. Here we implemented individual-based simulations with demographic noise, but we have examined numerically the same systems with environmental noise and make sure that the main results still hold.

In the simplest models of population dynamics the size of the community reaches equilibrium, and extinction happens due to large fluctuations (see Figure 0, upper panels). To understand what controls the chance of extinction let us take a look at one specific and well-studied model of this type, the logistic growth (*33*). The results of this model will provide us with a general (not model-specific) insight about the chance of extinction for an isolated population.

The simplest deterministic model for well-mixed (single patch) population dynamics is the continuous time logistic equation,

(1) $$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right).$$

X, the population size, reaches equilibrium at carrying capacity K. For the deterministic differential equation (1) K is merely a scale factor: in fact, one can absorb it into the definition of the effective population density by defining y = x/K, obtaining the same equation for y with K=1. However, in reality the carrying capacity of the system corresponds to an integer that reflects the equilibrium number of individuals, thus determining the chance of extinction due to demographic fluctuations (*34, 35*).

Let us consider now a specific stochastic process that corresponds to Eq. (1). If A is a single individual, the stochastic-logistic process involves the transitions:

(2) $$\begin{gathered} \mathrm{A} \xrightarrow{\alpha} 2\mathrm{A} \\ \mathrm{A} \xrightarrow{\gamma} \varnothing \\ 2\mathrm{A} \xrightarrow{\beta} \varnothing \end{gathered}$$

where α, β and γ are the rates of birth, death and competition related death, respectively. This process satisfies a master equation in which P_n stands for the chance to find n A-s (*36*):

(3) $$\frac{\mathrm{dP_n}(t)}{\mathrm{dt}} = \alpha\left[-nP_n + (n-1)P_{n-1}\right] + \gamma\left[-nP_n + (n+1)P_{n-1}\right] + \frac{\beta}{2}\left[-n(n-1)P_n + (n+1)(n+2)P_{n+2}\right]$$

The process (2) corresponds to Eq. (1) in the following sense: defining the average number of individuals at time t, $\overline{\mathrm{n(t)}} \equiv \sum_n n\mathrm{P_n}(t)$, the time evolution of this quantity is given by

(4) $$\frac{d\bar{\mathrm{n}}}{\mathrm{dt}} = (\alpha - \gamma)\bar{\mathrm{n}} - \beta\overline{\mathrm{n(n-1)}} = (\alpha - \gamma)\bar{\mathrm{n}} - \beta\bar{n}(\bar{n} - 1) - \beta \cdot Var(n).$$

If the variance is small (which is the case when the population is large), this time evolution converges to (1) with $r = \alpha - \gamma + \beta$ and $K = \frac{\alpha - \gamma}{\beta} + 1$. The +1 shift in the value of K reflects the absence of self-competition, such that the competition term in (4) vanishes when there is only one animal. In fact in most cases $Var(n) \approx n$ (see Appendix A), with this $r = \alpha - \gamma$ and $K = (\alpha - \gamma)/\beta,$ but the differences are irrelevant for the discussion below. K is the equilibrium number of individuals in the following sense: when the number of individuals is smaller than K, the rate of birth (times the population size) is larger than the overall rates of death and competition, so it is more probable that the population will grow in the next timestep. The opposite is true when the system occupancy is larger than K.

What is the typical timescale for extinction of such a system under demographic noise? A simple argument suggests that if we have K individuals in the system, extinction occurs when K death/competition events happen without any birth. Clearly, the chance for such a giant fluctuation falls exponentially with K, i.e., like $\exp(-\mu K t)$ where μ is some constant (*35*). Although one may suggest many other routes to extinction, the basic insight holds true: recent analyses (*36-39*) allows one to find exactly the coefficient μ, and even to calculate the pre-exponential dependence.

However, this intuitive argument [see also (*36, 38-40*)] is true only if the carrying capacity K is large enough. With demographic noise, the number of individuals at equilibrium is not exactly K. Instead, the chance to find N individuals is distributed, more or less normally, around K [this "Gaussian approximation" is in the core of the Ω expansion suggested in (*41*); for its limitations see (*36*)]. The standard deviation of this Gaussian is growing like the square root of K, with a coefficient determined by the Lyapunov exponent of the fixed point, $r = \alpha - \gamma + \beta = \frac{K(\alpha - \gamma)}{K - 1}$; for small r and large K, the STD σ scales like $\sigma \sim \sqrt{K/2r}$. [This result has been obtained using a moment truncation approximation. For a detailed description of the method and a comparison with other techniques, see Appendix A.] Within this regime, i.e., when $|K - n| < \sigma$, the occupancy fluctuations are more or less unbiased, since the differences between the overall birth and the overall death rates are tiny. When $K < \sigma$, thus, the dependence of the system lifetime on K is much slower than exponential: for example if there is no bias at all (r=0) the typical time to extinction scales like $K^{3/2}$ (*42*). This phenomenon manifests itself in Fig.1, where the transition from non-exponential dependence of the lifetime on K to exponential stability is demonstrated for different values of the Lyapunov exponent r.

While we have considered here only one specific example, the basic moral holds true for any deterministic dynamics that support an attractive manifold (a stable fixed point, a limit cycle or even a chaotic orbit, as long as these orbits do not "graze" the zero occupancy state). All these systems may be in the extinction robust state, where the time to extinction is growing exponentially with the occupation numbers (if these numbers are varying in time, with the infimum of the population size). This is the case as long as the distance between the infimum and zero is large with respect to σ. Otherwise, the system is in the extinction prone state and its lifetime grows with its carrying capacity in a slower, non-exponential manner.

For some classes of deterministic models there is no extinction-robust sector even if the typical occupation numbers are large. These are the dynamics that admit zero infimum, like the Nicholson-Bailey map for host-parasitoid interaction or the discrete version of the logistic equation, the logistic map

$$x_{t+1} = rx_t\left(1 - \frac{x_t}{K}\right) \tag{5}$$

for r=4 (see Fig. 2). An isolated population that follows these dynamics is always extinction-prone.

In the extinction robust phase, the time to extinction is growing exponentially with its carrying capacity. This implies that the buffering effect – reduction of the relative amplitude of fluctuations - is very strong, and in the typical scenario it will, most probably, dominate the coherence effects. On the other hand, when the system is extinction prone the effect of buffering is relatively weak, and thus other mechanisms that affect stability may become more important.

2. *Spatial structure: coherence and regional extinction*

Given the analysis of local population dynamics provided in the last section, we now move on to consider ecological communities that are made of spatially segregated colonies, or habitat patches, with some level of migration between them. Transfer of individuals buffers the system, reduces the effect of fluctuations and allows for recolonization of empty patches. Accordingly, construction of "conservation corridors" (*1*) among habitats is considered a possible human intervention that may decrease the chance of extinction for an isolated population. Habitat fragmentation, on the other hand, poses a danger to the stability of an eco-community. In this section we implement a simple, two-patch example, to explain the conditions under which these suppositions are valid and to exemplify the case where they become wrong. We will try to emphasize the difference between equilibrium and time-varying local dynamics. For time varying systems, spatial coherence may be a crucial factor in the persistence of a spatially structured population.

Let us consider a community on two isolated and identical patches. Transfer of animals is not allowed, so any local community lives and perishes according to the principles sketched in the last section. If the typical lifetime of a single local habitat is τ, the lifetime of two isolated patches will be roughly the same. (To be more rigorous, the time until extinction of both colonies is the maximum of two numbers drawn from the same random distribution, this number depends only logarithmically on the number of patches).

Now what happens if one introduces a symmetric, density independent migration between the two patches? In the extreme case where the migration is much faster than any other process in the system, both populations are well mixed. In the absence of self-interactions, [see discussion of the "hydrodynamic limit" in (*30*)] one may consider both patches as a single colony with typical occupancy which is twice as much as a single patch. This increase of the effective population leads to an increase in the sustainability of the system. If the dynamic is extinction robust and the persistence time of a single patch is $\exp(\mu K t)$, the well mixed system will survive until $\exp(2\mu K t)$, i.e., the persistence time is growing exponentially. On the other hand, if the system is in the extinction prone regime, its persistence time would grow with the effective population size but the growth is much slower.

Another migration-dependent effect may take place when the local dynamics are varying in time (i.e., have some internally driven variations, periodic or oscillatory, either in a regular or in an erratic/chaotic way). In that case subpopulations oscillate between large and small abundance. As we mentioned above, the chance of extinction is usually determined by the lowest level (infimum) of the population size along time. If the dynamics of the two patches is incoherent its neighbors may supply immigrants when the local population is in danger. Even better situation (*43, 44*) is that of negatively correlated spatial dynamics (checkerboard), when a decrease of the population on one patch is accompanied by an increase on the other patch. This scenario occurs at intermediate levels of migration and depends on the existence of constant perturbations or intrinsic noise that avoid global synchronization (*45, 46*). The loss of spatial synchrony may even lead to the appearance of a new attractive orbit that does not exist in the single-patch dynamics: a phenomenon that was discovered in the context of coupled lattice maps (*47, 48*) and then was observed in some ecological models (*49-51*). An increased stability in incoherent coupled systems has been demonstrated also for a wide variety of stochastic models (*11, 43-46*).

Decoherence stabilization of this kind may take effect only in the intermediate migration regime. When the rate of individual transfer is too strong the system becomes coherent and the stabilizing effect of decoherence is lost. Accordingly there are two scenarios: if the buffering effect is stronger, an increase in the migration rates or the connectivity of the system always helps to decrease the chance of extinction (*21*). On the other hand when the coherence effect is stronger the chance of extinction is minimal at some intermediate level of migration, and a further mixing between colonies is harmful. In the first case the persistence is an ever increasing function of the migration rate and in the second case there is a typical bell (hump) shape of the persistent vs. migration curve, as depicted in Fig. 3. Clearly the role of decoherence stability is more important when the local dynamics is extinction prone since in this regime the buffering effect is much smaller.

In practice, most of the conservation efforts have to do with eco-communities that are locally extinction prone. If an isolated community is unstable, the persistence of the population depends on immigrants from nearby local communities. One of the common assumptions is that an increased rate of migration or an improvement in the connectivity among patches is good for the system persistence (*52*). However, as pointed out by (*10*), this intuitive argument may be misleading: communities may go extinct as a result of increased movement that induces coherence and exposes the metapopulation to the danger of regional-scale death. In the last two sections we have identified the dangerous zone: the regime of parameters where the system is extinction prone and the local dynamics is time varying. In the next section we consider the stochastic patch occupancy model (SPOM), and show why it cannot predict the coherence mediated regional extinction.

3. SPOM and the two-state approximation:

One of the main goals of ecological modeling and the analysis of extinction probabilities is the ability to predict, or to evaluate the chance for extinction, based on data collected in field studies. However, for many types of plants and animals it is very hard to collect accurate and long datasets about the number of individuals per habitat patch through time. For that reason, experts have developed the stochastic patch occupancy model and the inference techniques, like SPOMSIM, that are based on it. To analyze the dynamics of a metapopulation using this model one needs only presence/absence data. This, together with some general assumptions about the relations between local persistence, patch area and connectivity, allows one to calculate the expected time to extinction with reasonable accuracy.

SPOM characterizes a habitat patch as either empty or occupied, i.e., it neglects the intra-patch dynamics. Except for the colonization (settlement) and the extinction stages, the population is assumed to be more or less fixed. This assumption may be justified if colonization and extermination both happen during short time scales, i.e., after a successful colonization the local community reaches its carrying capacity quite fast, and extinction happens due to large fluctuations that, again, occur during a relatively short period. If this is true one can implement the two-state approximation: the system jumps quite rapidly from the empty to the occupied state and vice versa, and spends its "occupied" phase fluctuating around its carrying capacity. In figure 4, this property is demonstrated for a stochastic-logistic growth; indeed the typical occupation (sojourn) time is much larger than the settlement/extinction periods.

To obtain a quantitative measure for this separation of timescales for stochastic models, we can define the settlement time τ_1 as the period between the colonization (introduction of the first immigrant, or the first pair of immigrants for sexually reproducing animals, on an empty patch) and the time when the population first exceeds the carrying capacity K. The extinction period τ_2 is, correspondingly the time elapsed between the last crossing of K and complete extinction. If τ is the overall lifetime of the colony (from colonization to full extinction),

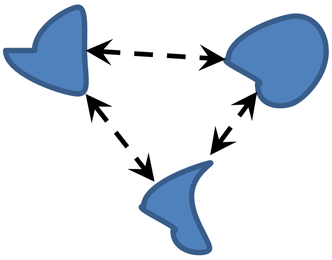
$$f = \frac{\tau_1 + \tau_2}{\tau} \qquad (6)$$

measures the fraction of the settlement + extinction stages compared to the overall lifetime. When $f \ll 1$ there is a clear separation of timescales; when f is close to one there is no such separation and the intra-patch dynamic is important. In the inset of Fig. 5 one can see a histogram of *f* values gathered from many numerical experiments for the stochastic-logistic dynamics in the extinction-robust regime; the *f* values are definitely small.

This approximation works very well for extinction robust system, but for extinction-prone scenarios its applicability is questionable, as demonstrated in Fig 5 (main panel). Here there is no clear separation of timescales, and the negligence of the intra-patch dynamics becomes questionable. The separation of timescales and the neglectance of the intra-patch dynamics in SPOM (see Figure 7) are very good approximations for local dynamics that admit an equilibrium population (not time-varying) and are extinction-robust. Effects of decoherence are important in the opposite regime: when the local dynamics is time varying and extinction-prone. As a result, SPOM cannot detect or predict the effects of coherence, and in particular it always predicts that increased migration/connectivity will enhance the eco community persistence. The situation is summarized in Table 1.

Fig. 6 depicts the average time to extinction, as obtained from an individual based model (see next section for details), versus the migration rate for different connectivity matrices. The typical bell-shape of this curve indicates that the lifetime first increases with migration, reflecting the stabilizing buffering effect, then decays at large rates of migration, as the effect of coherence becomes important. Moreover, keeping the migration at the same level and increasing the connectivity leads to a sharp decrease in the system persistence time for intermediate rates of migration. Before constructing a corridor between the corners of the square one would like to be sure that the system is not on the intermediate/large migration rate regime, where such an intervention may cause only harm. In the next section we present the simple individual based model we have implemented in this simulation, and then will show how to detect the coherence effects using occupancy data.

4. The individual based model



To study the capabilities and the limitations of the two-state approximation implemented in SPOM, a comparison is made between its results and simulations of individual based dynamics. We have used a simple island model (see illustration, right), assuming a population dynamics with non-overlapping generations. In the spirit of the Hamilton-May model (*24*), each generation involves two consecutive steps. The ''local reaction'' (birth, death, competition etc., at which any patch is affected only by the local population), is followed by a density independent ''migration'' (dispersal) step, where individuals are allowed, with a certain probability, to leave their local community and migrate to another patch. There is no dispersal cost and any emigrant reaches its chosen destination. The details of our numerical algorithm are given in (*43, 44*).

Another simplification we have made is that all patches have the same area (or carrying capacity K). This does not makes a lot of difference, since for the randomly scattered spatial patterns considered below (see Fig. 7), as nearby patches with high migration rate between them may be considered as a single, large habitat.

For the sake of convenience we have chosen a local dynamics that follows (on average) the Ricker map, $x_{t+1} = x_t \exp\left(r\left[1 - x_t\right]\right)$ (*53*). This map is widely used in ecological modeling, and is easy to simulate as (unlike the logistic map) there is no upper bound to the number of individuals and the map is smooth. The deterministic map supports either attractive orbit or chaotic trajectories, depending on the basic reproductive rate r. Adding demographic stochasticity to the map, it may be either in the extinction prone or in the extinction robust phase, depending on the occupation numbers, as explained above.

For the spatial system a two-step algorithm was implemented. Before the reaction step, the number of animals on the i-th site is $n_{i,t}$. Each of these individuals produces *s* offspring and dies. The chance of an offspring to survive competition and to reach maturity is

$$p = \exp\left(-\frac{sn_{i,t}}{K}\right). \tag{7}$$

The overall number of surviving offspring $n_{i,t+1}$ is taken from a binomial distribution, i.e., the chance to have $n_{i,t+1}$ successes in $sn_{i.t}$ trials with a probability *p* of succeed in any specific trial. The *expected* number of surviving offspring that reach maturity is

$$E[n_{i,t+1}] = sn_{i,t} \exp\left(-\frac{sn_{i,t}}{K}\right) = n_{t,i} \exp\left(\ln(s)\left[1 - \frac{sn_{i,t}}{K}\right]\right). \tag{8}$$

The local dynamics is thus equivalent, on average, to the Ricker map $x_{t+1} = x_t \exp\left(r\left[1 - x_t\right]\right)$ with the rescaled parameters r=ln(s), x = sn/K. This map is chaotic for r>2.6924.

After this reaction step comes a passive migration step: any mature animal may decide to stay at its local habitat patch with probability 1-ν, or to immigrate with probability ν. Upon migration it chooses its destination at random from all other patches with a probability that decays exponentially with the distance, or, in other simulations, it chooses its destination among all patches with equal probability. The algorithm repeatedly iterated this reaction-migration process.

As demonstrated in Figs. 3 and 6, the effect of decoherence on the sustainability is prominent in the individual based simulations, but the retrieval of the model and its parameters from the noisy field (or even experimental data) is an intricate task. One would like to have a tool that tells about the relative importance of decoherence to stability, a tool that utilizes presence/absence data only and is independent of the specific features of the underlying population dynamics. This tool is presented in the next section.

5. Identification of coherence effects with presence/absence data.

Running the individual based model for a while, we gathered the series $n_{i,t}$: the population on the n-th site at time t. We are using this set of result as a simulated data to be analyzed by SPOM. First, we replace $n_{i,t}$ by a presence/absence timeseries $\theta_{i,t}$ where

(9) $$\theta_{i,t} = \begin{cases} 1 & \text{if } n_{i,t} > 0 \\ 0 & \text{if } n_{i,t} = 0 \end{cases}.$$

See Fig. 7 where this binarization process is illustrated. For each site i at time t we have calculated also the connectivity

(10) $$S_i(t) = \sum_j \theta_{j,t} m_{i,j} ,$$

where $m_{i,j} = \exp(-\alpha d_{i,j})$. $m_{i,j}$ is the probability that an individual from j will immigrate to i, $d_{i,j}$ is the distance between the i-th and the j-th sites and α is the parameter that determines the typical distance traveled in a single migration event.

Monitoring the system along time we have a set of θ and S for any site and any time. We then mapped the dynamics into a memory-less, two-state Markov process. Such a process is defined by the parameters $P(1 \to 0|S)$ and $P(0 \to 1|S)$, the extinction and colonization probabilities given the connectivity of a patch. For a given S we have estimated $P(1 \to 0|S)$ by the number of extinction events observed for an occupied patch with connectivity S, divided by the total number of occupied sites with connectivity S. $P(0 \to 1|S)$ is, correspondingly, the estimated chance of colonization given S.

One of the fundamental assumptions of SPOM is about the relations between the extinction/colonization probabilities and the connectivity S. The authors of (*2*) have suggested a few possible expressions for these relations. For example, one of the possibilities mentioned is:

$$P(0 \to 1|S) = 1 - e^{-yS} \qquad P(1 \to 0|S) = \min\{1, \mu e^{-xS}\}. \tag{11}$$

Anyhow, all the expressions suggested presume that the dependence of the extinction/recolonization probabilities on S is *monotonic*: increasing the connectivity *always* increases the number of recolonization events and decreases the chance of extinction. Given this assumption, one should expect that the lifetime of the system grows when it becomes more connected: in particular the time to extinction must decrease with an increase of the migration rates, or when new corridors enhance the connectivity among patches. As we have demonstrated above (see Figs. 3 and 6) this is not the case for extinction prone and varying dynamics in the intermediate/high migration rate regime. In this case, when a system becomes more connected, nearby patches start to fluctuate coherently. As a result they all reach the low-density state at the same time, exposing the whole region to the danger of correlated extinction.

This effect manifests itself in Fig. 8. Here the dependence of the transition rates on the connectivity, as obtained from the individual-based simulation described above, is plotted against the connectivity S for two scenarios. In both cases the Ricker map has been implemented in the extinction-prone parameter regime, with a spatial structure that is statistically identical to the one presented in Fig. 7. To get smooth lines of P vs. S we have to average over many spatial configurations, as in one set of 25 patches the number of possible connectivities is limited, but the general trend – decay or growth with S – may be identified even for a single realization.

In the first numerical experiment we have chosen the number of offspring *s* such that the corresponding deterministic Ricker map admits an equilibrium stable fixed point (period-1 orbit, as in Fig. 0, upper panels). The second set of simulations have used the same "geography" (identical statistical properties for the spatial arrangement of patches), but now with s that corresponds to a chaotic trajectory.

In the first case the intra-patch dynamics allows no variations in time, thus there is no effect of decoherence stabilization. Accordingly, migration is always a stabilizing factor: the chance of extinction is decaying monotonically with the connectivity and the chance of recolonization is always growing with S. The functional dependence is not exactly the one suggested in (11), but the general trend is identical.

If, on the other hand, the local dynamics are varying in time, above some level of migration the dependence of the extinction rate on S becomes nonmonotonic, or even reverses its direction. The reason, again, is that the large S events are usually related to a few nearby patches that fluctuate coherently and go extinct together when the migration rate is large. We have verified that this phenomenon is robust and appears also in the presence of spatially correlated environmental fluctuations (Moran effect) (*54*)

This feature may be used also as a *diagnostic tool*. Given a time series of $\theta_{i,t}$ and the distance matrix $d_{i,j}$ one can retrieve $P(1 \to 0|S)$ for some values of S. An observation of an increase of the extinction rate with S is an indication for the danger of regional extinction as nearby patches synchronize.

Although we do not present here a predictive technique that analyze a time series and calculates the chance of extinction, we can suggest a simple rule of thumb: if overcoherence is detected in the system, it is usually very easy to identify the synchronized subpopulations. Given that, it is recommended to construct conservation corridors somewhere else, and maybe it will be even useful to try to decrease the migration rate among these local habitats.

6. Discussion and Conclusions:

Throughout this paper we have tried to classify population dynamics models with respect to two important features of the local dynamics: the chance of extinction due to noise and fluctuations (extinction prone/robust), and the time evolution on the attractive manifold (equilibrium/varying in time). The chance of extinction in general is determined by two factors: one is the lowest (infimum) occupancy number encountered by the whole system along time and the other is the magnitude of fluctuations in the population size when the density is small.

An increase in the connectivity or the migration rate in a spatially extended system allows for recruitment of empty patches and is followed by a decrease in the amplitude of demographic fluctuations, as it increases the effective subpopulation size. This buffering effect makes the system less vulnerable to extinction events. On the other hand such an increased movement may lower the infimum occupancy as it induces coherence among patches. Thus, in varying systems it may be a destabilizing factor. The competition between buffering and coherence effects determines whether or not an increased movement (or connectivity) increases the lifetime of the system. In particular, when the dynamics is extinction prone (the population size is small in comparison with the fluctuations, as expressed by the standard deviation σ) the buffering effect is much weaker and there is a good chance that coherence effects are more important.

SPOM neglects the intra-patch dynamics, thus it may take into account only the buffering effects. As a result, within the SPOM framework sustainability always grow with migration. This outlook turns void in the extinction prone – varying regime, where the increase of spatial coherence may lead to the opposite behavior. We have demonstrated that by implementing agent-based models and comparing the effects of SPOM with the results obtained from these models for metapopulation persistence time.

Clearly, in any practical scenario it will be very hard to infer the "microscopic" parameters of dynamics, like birth/death rates and competition/predation parameters, from the field data. In the laboratory one may try to use recurrence plots [see (*15*) for example] but the inaccuracy of the measurements of population size, together with the effects of migration and external noise, make this mission almost impossible for subpopulations in the wild. To overcome this difficulty we have suggested here a technique that is based on the same presence/absence data used by SPOM. In the extinction robust, or for non-varying local dynamics, one would like to find if an increase in the connectivity of a patch is followed by a decrease of the chance of extinction. If this is not the case, it implies that coherence effects are important and the system may be on the brink of regional extinction: the common intuition of conservation ecologists turns upside-down; fragmentation increases the sustainability while corridors may cause harm.

Interestingly, the evolution of dispersal rates does not converge to an optimal solution. Our numerical experiments with Hamilton-May setup (*24*) – two species that differ only in their migration rate are competing – ended up with the victory of the "fast" species, even if the lifetime that corresponds to the higher level of migration was shorter. This implies that, in the coherence dominate regime, one should not assume that the natural state is somehow close to the optimum as it reflects the adaptation of dispersal rates along time.

Beyond its importance to sustainability assessment and management, there is a general theoretical interest in the identification of coherence effects in field data, after they have already confirmed in experiments (*12-18*). Again, we hope that our technique may be used for this purpose, with patch occupancy data that have been already collected or will be collected in the future.

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Appendix A

In this appendix we will show how to use an elementary moment truncation scheme in order to find the boundary between the extinction robust and the extinction prone regimes. The example studied here is the stochastic logistic growth process described in Eq. (2) above. For this process some analytic results are known and may be compared to our scheme. It is quite easy to generalize the qualitative part of the consideration presented here to many other models of population dynamics.

We begin with the exact master equation (3). From this we can derive an exact equation for the time evolution of the first moment, which is Eq. (4) above, but this equation involves the second moment $\overline{n^2(t)}$. The time evolution of the second moment is:

(A1) $$\frac{\mathrm{d}\overline{\mathrm{n}^2}}{\mathrm{dt}} = \alpha\left(2\overline{n^2} + \overline{n}\right) + \gamma\left(-2\overline{n^2} + \overline{n}\right) - 2\beta\left(\overline{n^3} - 2\overline{n^2} + \overline{n}\right)$$

This equation depends on the third moment of n. However, if K is large enough the P_n is almost a perfect Gaussian around K, so the skewness $\overline{\left(n - \overline{n}\right)^3}$ is negligible. Plugging

(A2) $$\overline{n^3} = 3\overline{n^2}\,\overline{n} - 2\overline{n}^3,$$

one obtains

(A3) $$\frac{\mathrm{d}\overline{\mathrm{n}^2}}{\mathrm{dt}} = \left(\alpha + \gamma - 2\beta\right)\overline{n} + (2\alpha - 2\gamma + 4\beta)\overline{n^2} + 4\beta\overline{n}^3 - 6\beta\overline{n}\,\overline{n^2}.$$

Eq. (A3) and (4) are now a closed set of nonlinear equations from which the standard deviation of the Gaussian, $\sigma = \sqrt{\overline{n^2} - \overline{n}^2}$, may be extracted. Expressing the results in terms of K, the carrying capacity, and r, the Lyapunov exponent, one finds that for large K-s

(A4) $$\sigma = \sqrt{\frac{2+r}{2r}K}.$$

Accordingly, the transition from the extinction prone to the extinction robust regime happens at

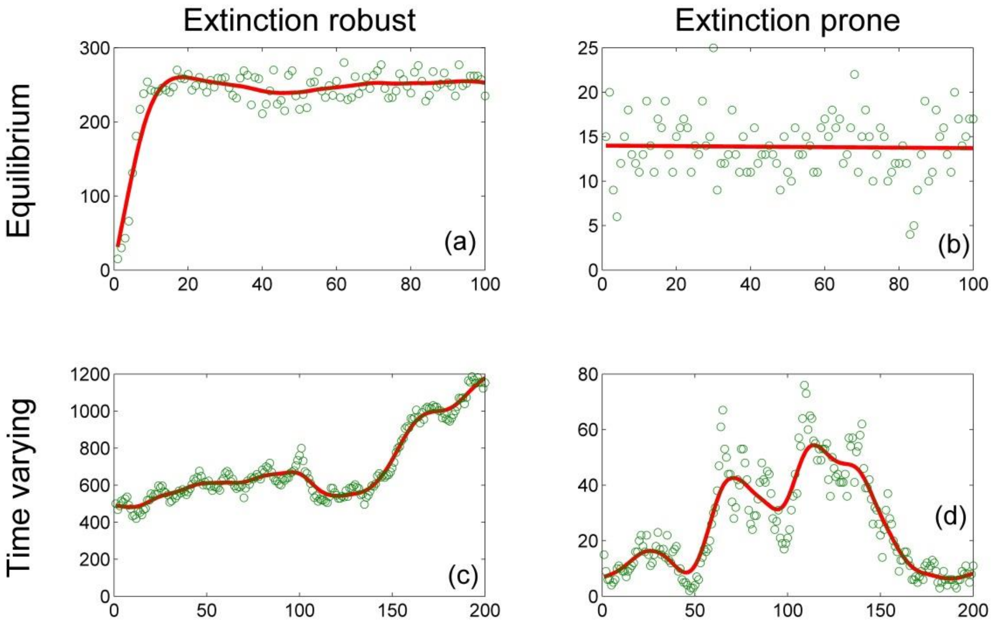
(A5) $$K_c = (2 + r)/r.$$

In (*55*) the authors have used a much more sophisticated WKB technique in order to evaluate the extinction times, and this birth-death-competition model is considered in the third section. In the WKB language the chance of extinction is given by the "action" S (the assumption is that S is large), and the theory breaks down in the extinction prone regime which occurs when S=1. With the parameterization used here, the WKB analysis of (*55*) predicts a transition for

(A6) $$K_{c,WKB} = \frac{\ln(1 - r/2)(r-2) - 3r/2}{\ln(1 - r/2)(r-2) - r}.$$

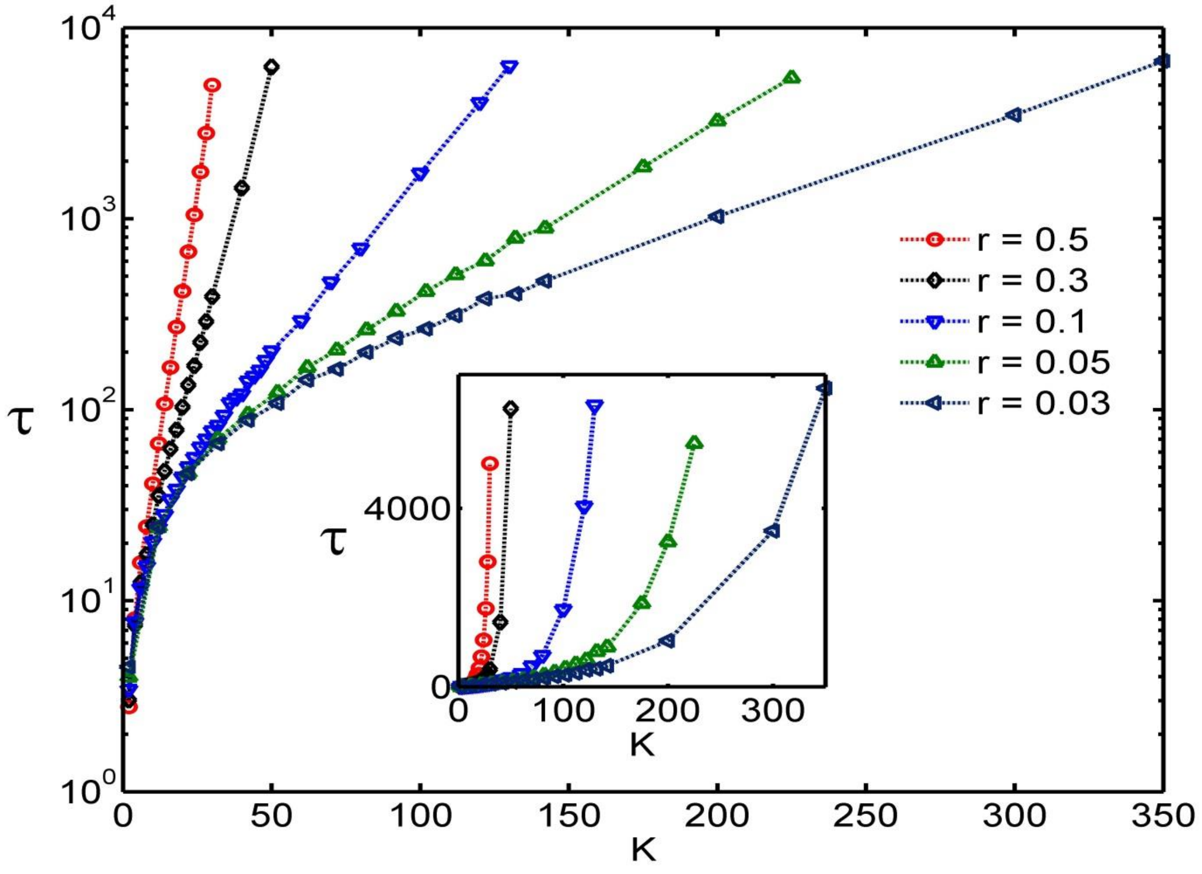
To the first order in r (A5) and (A6) coincides, and all over the relevant region 0<r<1 the difference never exceeds 12%.

Figure 0



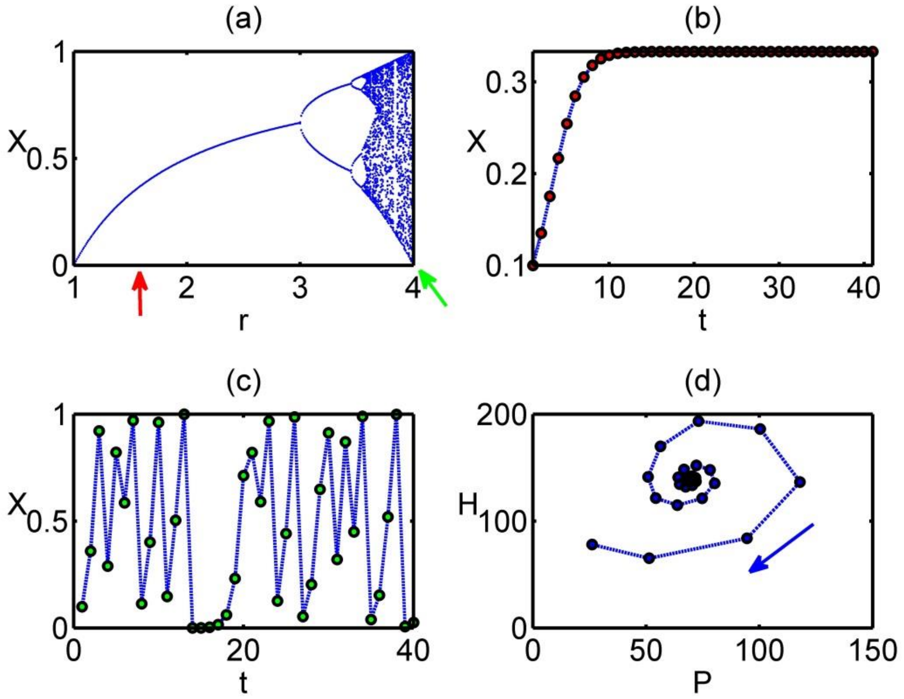
Four representative scenarios of the noisy dynamics of an isolated population. All panels show population number (an integer) vs. time (arbitrary units). In panel (a) we have simulated the logistic map in the regime where it supports an attractive fixed point (r=2) and with carrying capacity K that allows for approximately 250 individuals. Simulating the system with demographic noise (see section 4 for the details of the numerical procedure) we obtain a faked dataset for 100 seasons (green circles). When we smear out fluctuations using Matlab's cubic smoothing spline (csaps) the red line, which reflects the trends associated with the deterministic dynamics, emerged. Panel (b) shows the same for carrying capacity of about 15. The system (b) is extinction prone: the width of fluctuations is comparable with the steady state population, thus the time to extinction is relatively low. (a) is extinction robust: the fluctuations are small relative to the steady state population, to reach extinction one should wait for giant fluctuation that never happens on reasonable timescales. Panels (c) and (d) were generated in the same way, now using the deterministic Lotka-Volterra equations that generate internal population cycling (the predator population is shown). What determines not the chance of extinction is the strength of the fluctuations when the system reaches its lower population states (note that, incidentally, here the fluctuations are stronger close to the extreme values of the trajectory). While (c) imitates a time-varying extinction robust system, (d) is extinction prone.

Figure 1



The transition from the extinction prone to the robust regime. We have simulated the dynamics of an isolated population subject to the stochastic processes $A \xrightarrow{\alpha} 2A$ $A \xrightarrow{\gamma} \emptyset$ and $A + A \xrightarrow{\beta} \emptyset$, using the Gillespie individual based algorithm (*56*). One of the parameters determines the overall timescale, and the two others determine the carrying capacity $K = (\alpha - \gamma + \beta)/\beta$ and the Lyapunov exponent $r = \alpha - \gamma + \beta$. A single run starts with $n(t = 0) = K$ individuals, and stops when the population goes extinct due to demographic fluctuations. Here the average time to extinction τ versus the carrying capacity K for different values of the Lyapunov exponent r, both in logarithmic (main figure) and in normal (inset) scale. For large K the lifetime grows exponentially with K (straight line in the log scale, main): this is the extinction prone regime. For small K, on the other hand, the growth is slower than exponential (inset). The transition from the extinction prone to the extinction robust (exponential) regime appears at larger K values for smaller Lyapunov exponent r.

Figure 2

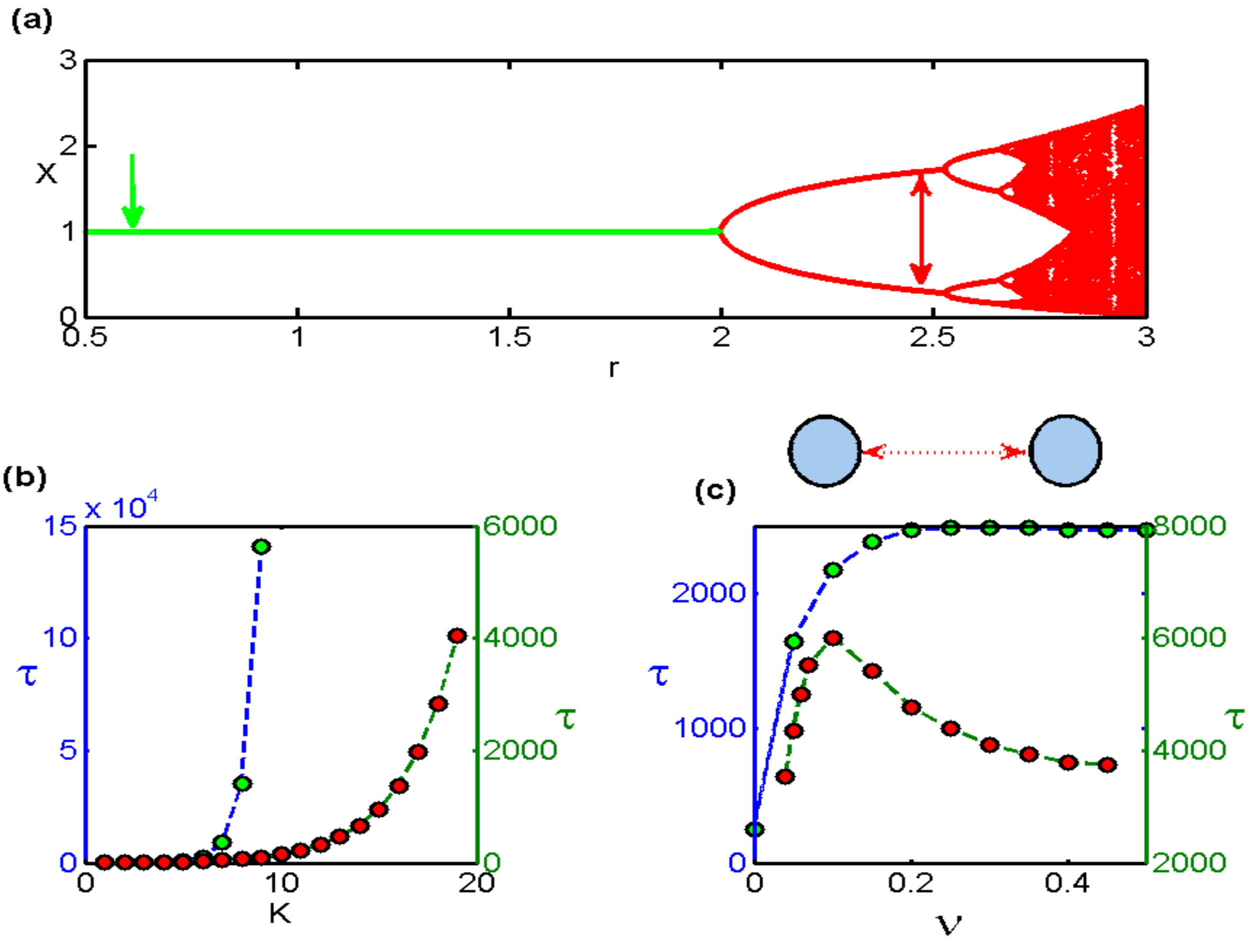


Various prototypes of the deterministic dynamics. The logistic map, $x_{t+1} = rx_t(1-x_t)$, supports an attractive, period one orbit for small r, as seen in the bifurcation diagram in panel (a). For the value of r indicated by the red arrow, the deterministic dynamics supports an attractive fixed point: starting from a small value of x the population grows and saturates [panel (b)]. In this range of parameter the stochastic dynamics may be either extinction prone or extinction robust, depending on the actual number of individuals associated with the steady state. As there are no time variations in the population size, coherence along spatial domains plays no role. For higher values of r the system supports more complicated attractive orbits and even chaotic trajectories. For these parameters also the dynamic may be either extinction prone or extinction robust, but now the population varies along time and spatial coherence effects may become important. For r=4 (green arrow) the system is always extinction prone as the infimum of the deterministic trajectory is zero, as depicted in panel (c). Another example of deterministic dynamics that is always extinction prone is provided by the Nicholson-Bailey host parasitoid model

$$H_{t+1} = cH_t e^{-\gamma P_t} \qquad P_{t+1} = qH_t\left(1-e^{-\gamma P_t}\right)$$

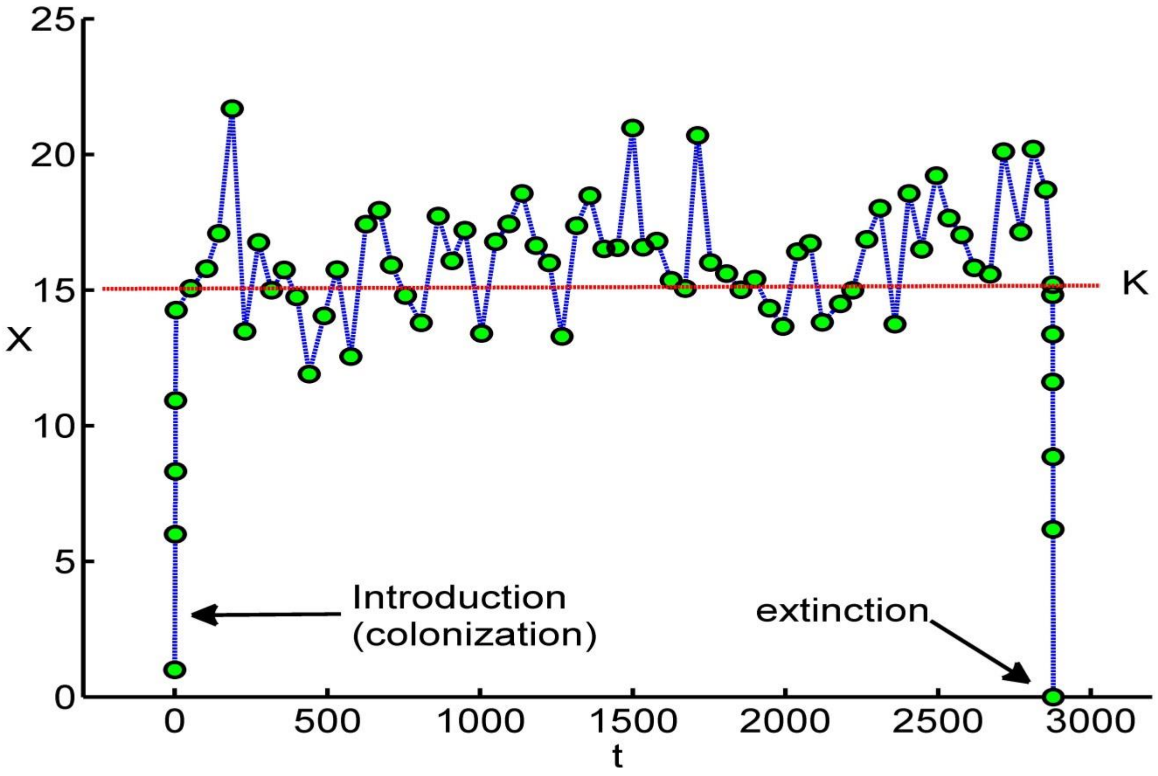
that supports ever growing oscillations, see panel (d).

Figure 3



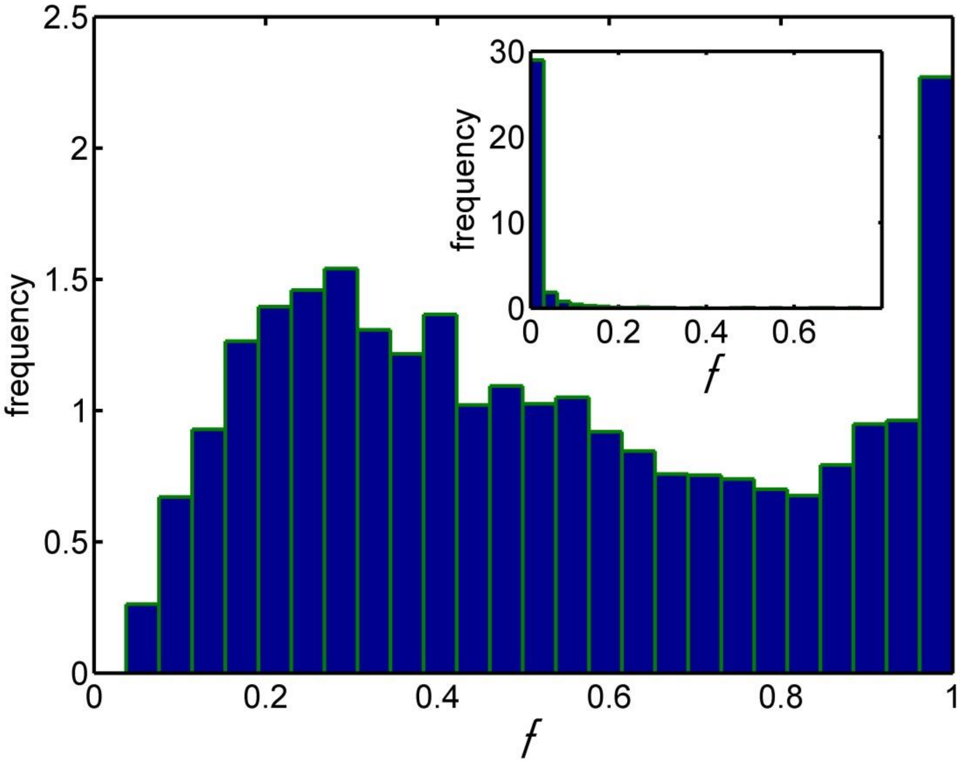
Time to extinction for two-patch system with stable (green) and varying (red) intra-patch dynamics. An agent based process that corresponds to the Ricker map (see section 4 for details) was simulated on each patch, where the value of s (the number of offspring per individual) corresponds to the regime when the map supports an attractive fixed point (r = 0.69, green arrow) or an attractive period-2 orbit (r = 2.48, red arrow), as indicated on the bifurcation diagram (a). The time to extinction for a local community is a monotonic increasing function of the carrying capacity K, as indicated in panel (b). However, when the rate of individual transfer between patches, ν, is varied, the lifetime grows monotonically for the stable dynamics (panel c, green, K=4) but shows the typical bell-shape for the two-state system (panel c, red, K=15). In a time-varying intra-patch dynamics the stability depends very much on the level of decoherence between the two patches. When the migration rate is large the two patches synchronize and reach the low population state at the same time, increasing the risk that both of them go extinct simultaneously.

Figure 4



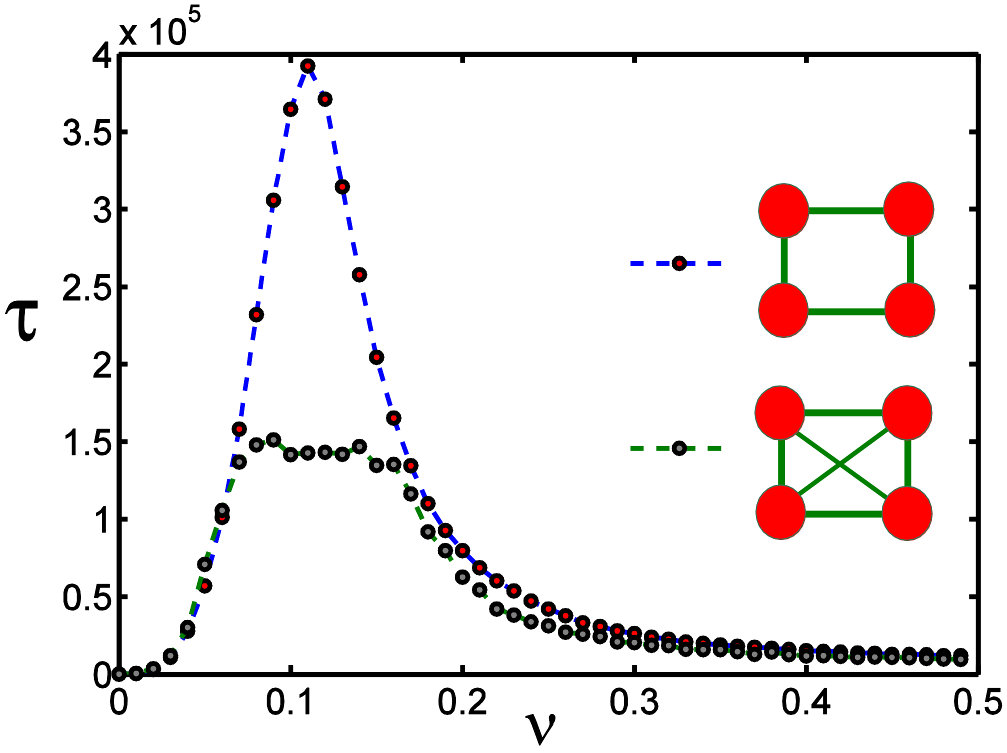
A typical turnover event for a single patch with extinction robust intra-patch dynamics. When the first immigrant arrives, a colony is established (reaches the carrying capacity, red line) on a short timescale. This colony persists for a relatively long time, until an extinction event happens, again quite rapidly. The figure here shows the results for the stochastic-logistic process (Eq. 2). Run starts with one individual, and ends up when there are no animals anymore. We have used the parameters $\alpha = 1$, $r = 0.99$ and $K=15$. The average number of agents, X, satisfies the logistic equation (1), where K sets the typical number of agents during the stable period. Note that the green points reflect a running average over small intervals of time; in reality the fluctuations induced by demographic stochasticity around the stable state are larger and faster for this K.

Figure 5



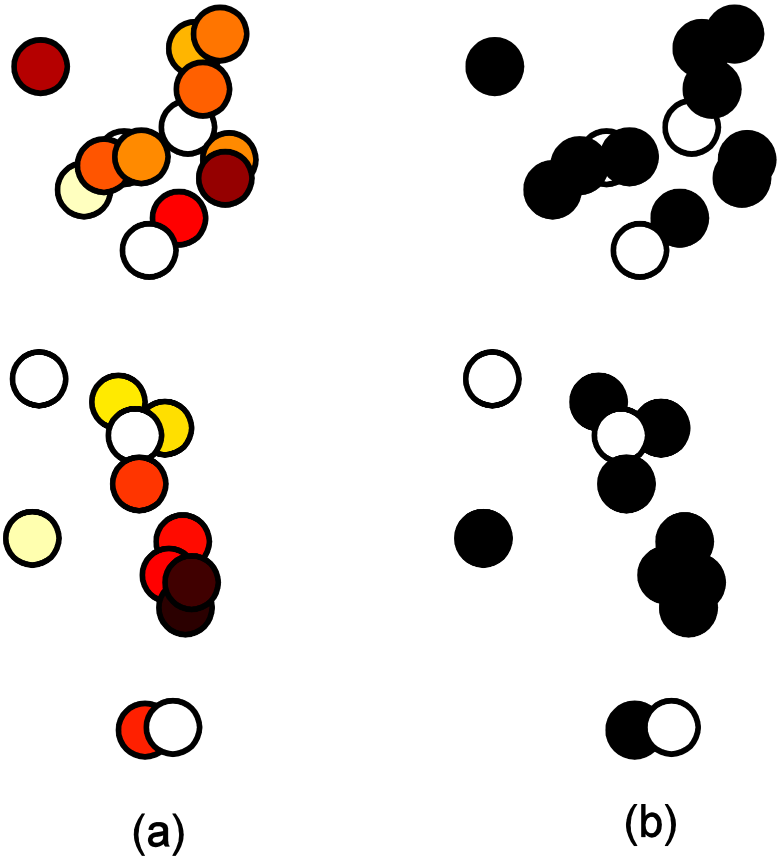
A histogram showing the probability that the system spends a fraction *f* of its lifetime in the settlement and extinction stages (as defined in Eq. 6). The histogram showing the frequency of *f* values for the stochastic-logistic model with K=15, all runs start with one individual. The inset shows the resulting distribution for r=0.99, while the main figure is for r=0.01 (note that one can change the rates of the stochastic process (2) and vary r while keeping the carrying capacity fixed). Runs for which the system went extinct before reaching K (colonization failure) were omitted from the statistics. For the r=0.99 case (inset) the population dynamics was exemplified in Fig. 4, and indeed one observes that the colonization and extinction times are both much shorter than the sojourn time when the population fluctuates close to its carrying capacity. This is not true anymore when r = 0.01: although the carrying capacity remains the same, it is much less "attractive" and fluctuations are larger.

Figure 6



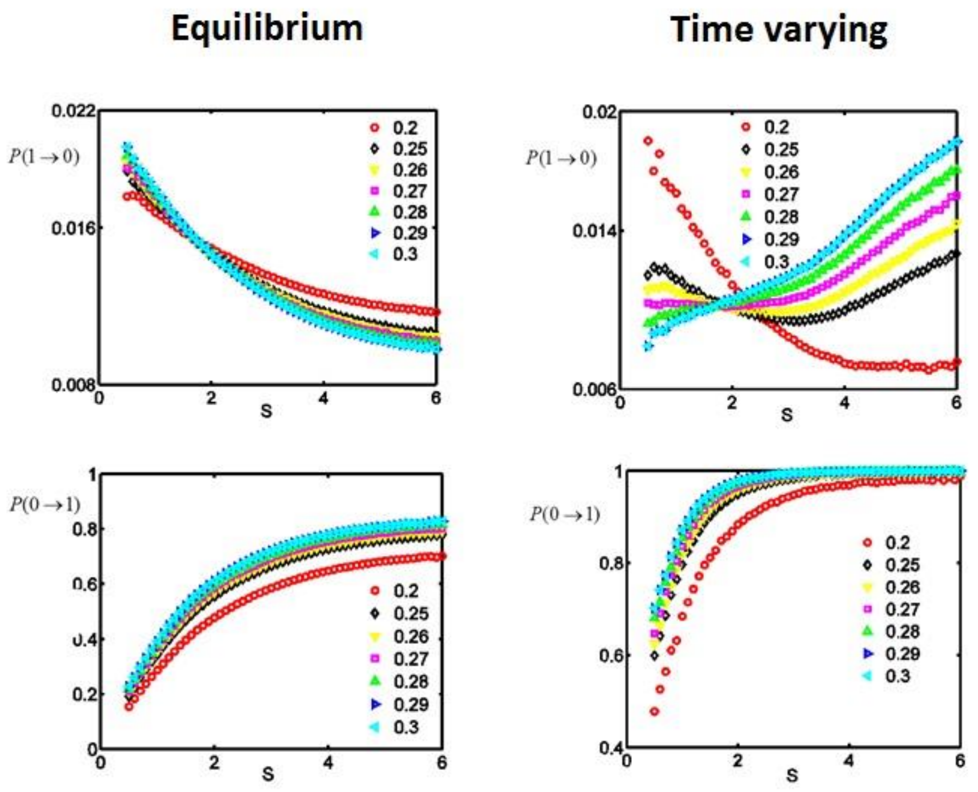
Persistence time of a metapopulation with extinction prone local patch dynamics. Shown here is the average time to extinction for a four patch system, with ring (red circles, blue dashed line) and global (grey circles, green line) connectivity. The individual based simulation procedure is described in the methods section. For small migration rates ν the lifetime of the system increases with the migration since it allows for recolonization and avoids the accumulation of local extinctions. On the other hand above ν=0.07 migration becomes a destabilizing factor, as it leads to overall coherence among patches and to global extinction. This leads to the hump shape that characterizes the lifetime vs. migration curve. Increasing the connectivity without changing the migration rate (global migration, grey) makes the system **less** sustainable for intermediate and high migration rates. The simulations were carried out for the stochastic Ricker dynamics with K=12 and s=17.

Figure 7



SPOM vs. IBM: an illustration of distinct habitat patches for 25 randomly allocated patches. The left panel shows a snapshot of the metapopulation where the color indicate the local population density: darker color stands for densely populated patch, while diluted populated patch marked by light colors. The right panel shows the same snapshot from SPOM point of view where black color present occupied patches and white is an empty one.

Figure 8



The chance of extinction, $P(1\to 0)$, and recolonization, $P(0\to 1)$, for a local community as a function of the connectivity S in the extinction prone regime for equilibrium (left) and time varying (right) dynamics. The individual based model of section 4 has been utilized with the Ricker map with r = 1.79 (equilibrium, attractive fixed point) and r = 2.8 (chaotic regime). Simulation was performed with different levels of migration, from weak (ν=0.2, red circles) to strong (ν=0.3, light blue triangles), according to the migration procedure explained in the text. The spatial arrangement of patches is the one shown in Fig. 7. When the intra-patch dynamics admits equilibrium value $P(1\to 0)$ decreases with the connectivity as expected. On the other hand for time varying local dynamics the chance of extinction may grow with S, at least for large migration rates. This nonmonotonic behavior indicates that the stability of the system depends on decoherence among local communities, and that an increase in the connectivity of the system may be harmful.

Table 1

Buffering effect (see section 1) Coherence effects (see section 2)	**Extinction robust** Strong buffering effect	**Extinction prone** Weak buffering effect
Equilibrium Occupied patches are more or less at the same state, up to fluctuations.	One equilibrium state. Clear separation of timescale, f<<1. Fits the assumptions of SPOM.	$f \sim 1$, no separation of timescales, but coherence effects are not important. SPOM still applicable (Fig 8, left)
Time-varying Incoherence may improve for sustainability	Intra-patch dynamics is nontrivial. The two-state approximation may become problematic. Buffering effect is large.	Regional extinction zone: Buffering effect is small, Spatial incoherence may become a crucial stabilizing factor. SPOM may fail (fig 8, right)

A table showing the different regimes discusses along this paper, categorized according to the local dynamics (each box is refers to its corresponding panel of Figure 0). In section 1 these dynamics were classified according to the buffering effect, i.e., the dependence of the persistence time on the carrying capacity: in the extinction robust regime this dependence is exponential and the buffering effect is very strong, while in the extinction-prone case this effect is much weaker. The distinction between equilibrium and time-varying systems is emphasized in section 2; in time-varying dynamics regional extinction may appear if all patches oscillate coherently and reach the infimum population at the same time. The analysis suggested by SPOM is based on the assumption that the dynamics may be projected on a two-state (empty/occupied) for each local community, so it fits perfectly the robust-equilibrium regime. However our numeric shows that SPOM works also for extinction prone regime as long as the local dynamics has equilibrium density, and may fail only for extinction-prone /time varying systems.

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