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Temporal Autocorrelation Can Enhance the Persistence and Abundance of Metapopulations Comprised of Coupled Sinks

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ABSTRACT: In spatially heterogeneous landscapes, some habitats may be persistent sources, providing immigrants to sustain populations in unfavorable sink habitats (where extinction is inevitable without immigration). Recent theoretical and empirical studies of source-sink systems demonstrate that temporally variable local growth rates in sinks can substantially increase average abundance of a persisting population, provided that the variation is positively autocorrelated—in effect, temporal variation inflates average abundance. Here we extend these results to a metapopulation in which all habitat patches are sinks. Using numerical studies of a population with discrete generations (buttressed by analytic results), we show that temporal variation and moderate dispersal can jointly permit indefinite persistence of the metapopulation and that positive autocorrelation both lowers the magnitude of variation required for persistence and increases the average abundance of persisting metapopulations. These effects are weakened—but not destroyed—if variation in local growth rates is spatially synchronized and dispersal is localized. We show that the inflationary effect is robust to a number of extensions of the basic model, including demographic stochasticity and density dependence. Because ecological and environmental processes contributing to temporally variable growth rates in natural populations are typically autocorrelated, these observations may have important implications for species persistence.

Keywords: dispersal, autocorrelation, inflation, sink metapopulation, population persistence.

Understanding the interplay of temporal and spatial variability as drivers of population dynamics and how this interplay is modulated by dispersal are topics of fundamental importance in population and community ecology (Levins 1969; Levin 1974; Hanski and Gilpin 1991; Chesson 2000; Hanski and Gaggiotti 2004). In a heterogeneous landscape, local populations may persist in low-quality habitats (sinks) because of recurrent immigration from populations that persist in high-quality habitat (sources; Holt 1985; Pulliam 1988; Pulliam and Danielson 1991; Kawecki 2004). An increasing number of empirical examples of source-sink systems document temporal variation in the rate of population growth in sinks, with transient periods of positive growth in habitats that on average are sinks (Virgl and Messier 2000; Johnson 2004). An important dimension of temporal variation is its autocorrelation structure.

Fluctuations of abiotic and biotic factors are often positively autocorrelated through time (Schoener 1985; Steele 1985; Pimm and Redfearn 1988; Arino and Pimm 1995; Halley 1996; Gillman and Dodd 1998; Wigley et al. 1998; Pascual et al. 2000; Petchey 2000; Inchausti and Halley 2001). There is growing theoretical attention being paid to how autocorrelated variation influences population and community dynamics (Caswell and Cohen 1995; Ripa and Lundberg 1996; Kaitala et al. 1997; Petchey et al. 1997; Haccou and Vatutin 2003; Ripa and Ives 2003; Levine and Rees 2004). In closed populations that are regulated by density-dependent processes (Royama 1992), positively autocorrelated temporal variability in growth rates can endanger population persistence because these fluctuations can reduce abundances to low levels for long periods (Turelli 1977; Tuljapurkar 1982; Mode and Jacobson 1987; Rotenberg 1987; Foley 1994; Johst and Wissel 1997). In a metapopulation, where a species persists because of a balance between colonization and extinction, all else being equal, a factor that increases local extinction rates should endanger persistence. So temporal autocorrelation in local growth rates may be thought to harm metapopulation persistence.

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In this article, we suggest that there is another effect of temporal autocorrelation in local population growth rates that has a positive impact on metapopulation persistence, mediated via changes in local population size and the potential for colonization. The basic idea emerged from studies of population dynamics in source-sink environments. In a classical source-sink environment (Holt 1985; Pulliam 1988), one habitat patch (the source) contains a population that deterministically persists, with births exceeding deaths, providing emigrants that sustain a population in a second habitat (the sink) where deaths outnumber births. Recent theoretical analyses showed that in a sink with weak density dependence, positive temporal autocorrelation in growth rates can substantially enhance average population size—an effect dubbed the "inflationary" effect of temporal variation (Gonzalez and Holt 2002; Holt et al. 2003). With positive autocorrelation and temporal variation including some years in which populations grow, there are runs of good years and runs of bad years. Recurrent immigration into a sink population permits persistence through the bad times, which then allows the population to quickly capitalize on subsequent runs of locally improved conditions; if these runs are sufficiently long and density dependence is weak, the population transiently grows to large sizes. A time average over both good and bad times then gives an increase in average abundance. An experimental microcosm study of source-sink dynamics in the protozoan *Paramecium tetraurelia* (Gonzalez and Holt 2002), which manipulated the temporal pattern of local growth by varying temperature, demonstrated a substantial increase in the average size of a microbial sink population due to a positive autocorrelation in growth rates, as predicted.

We show here that the inflationary effect of autocorrelated temporal variation shown in single sinks maintained by immigration from a persistent source can also contribute to the persistence of metapopulations where all patches on average are sink habitats. We start by developing a discrete generation source-sink model (eq. [1]) that illustrates the inflationary effect of temporal variation on average abundance in a single sink habitat. We provide a heuristic argument as to why analyses of source-sink dynamics may illuminate the behavior of metapopulations and examine a metapopulation model (eqq. [9], [10]) where all patches are sinks. This model demonstrates that positive autocorrelation in local growth rates can facilitate metapopulation persistence, in the sense that temporal autocorrelation allows some metapopulations to persist that would otherwise become extinct with the same distribution of growth rates without autocorrelation. To assess robustness, we examine several extensions of the basic model, including local dispersal, spatial correlation, demographic stochasticity, and alternative patterns of density dependence. The inflationary effect is qualitatively robust to these modifications (although it may be quantitatively weakened). In these models, total population size tends to be maximized at intermediate dispersal rates, suggesting that the nonmonotonic effect of dispersal on population size noted by Hanski and Zhang (1993), Holt (1993), and Ives et al. (2004) may be widely applicable. We conclude by reflecting on ecological mechanisms that can generate local positive autocorrelation in growth rates and touch on practical implications of our findings.

Temporal Variation and Sink Population Dynamics

In a classic mainland-island, or source-sink, structure (fig. 1*A*), there is one habitat (the source) where a species persists indefinitely and another habitat (the sink) where the species would become extinct were its numbers not replenished by recurrent immigration from the source. A substantial literature exists exploring population dynamics in source-sink landscapes (e.g., Holt 1985; Pulliam 1988; Pulliam and Danielson 1991; Brawn and Robinson 1996; Ritchie 1997; With and King 2001; Kawecki 2004), typically assuming that sinks have constant conditions. Gonzalez and Holt (2002) and Holt et al. (2003) examined the effect of temporal variation in the growth rate of sink populations using continuous-time models and demonstrated that autocorrelated temporal variation in growth rates could substantially increase the time average of population size in the sink.

The model we consider here describes a species with discrete generations. In a given patch (the sink depicted in fig. 1*A*), the number of individuals in successive generations is described by

$$N(t+1) = R(t)N(t) + I(t) - E(t). \tag{1}$$

Here $N(t)$, $I(t)$, and $E(t)$, respectively, denote local abundance, immigration into, and emigration from the patch at time t. The growth rate $R(t)$ encompasses survival and reproduction and can in general be density dependent. Assume that $R(t)$ varies such that its geometric mean

$$G_R = \lim_{t\to\infty} \sqrt[t]{\prod_{\tau=0}^{t-1} R(\tau)} < 1.$$

This population, if closed to immigration, becomes extinct (asymptotically). Given recurrent immigration, the population persists. For simplicity, for the moment, we assume no emigration (as in fig. 1*A*). If we take the average over time of both sides of $N(t+1) = R(t)N(t) + I(t)$ (for a general discussion of time averaging, see Levins and Puccia

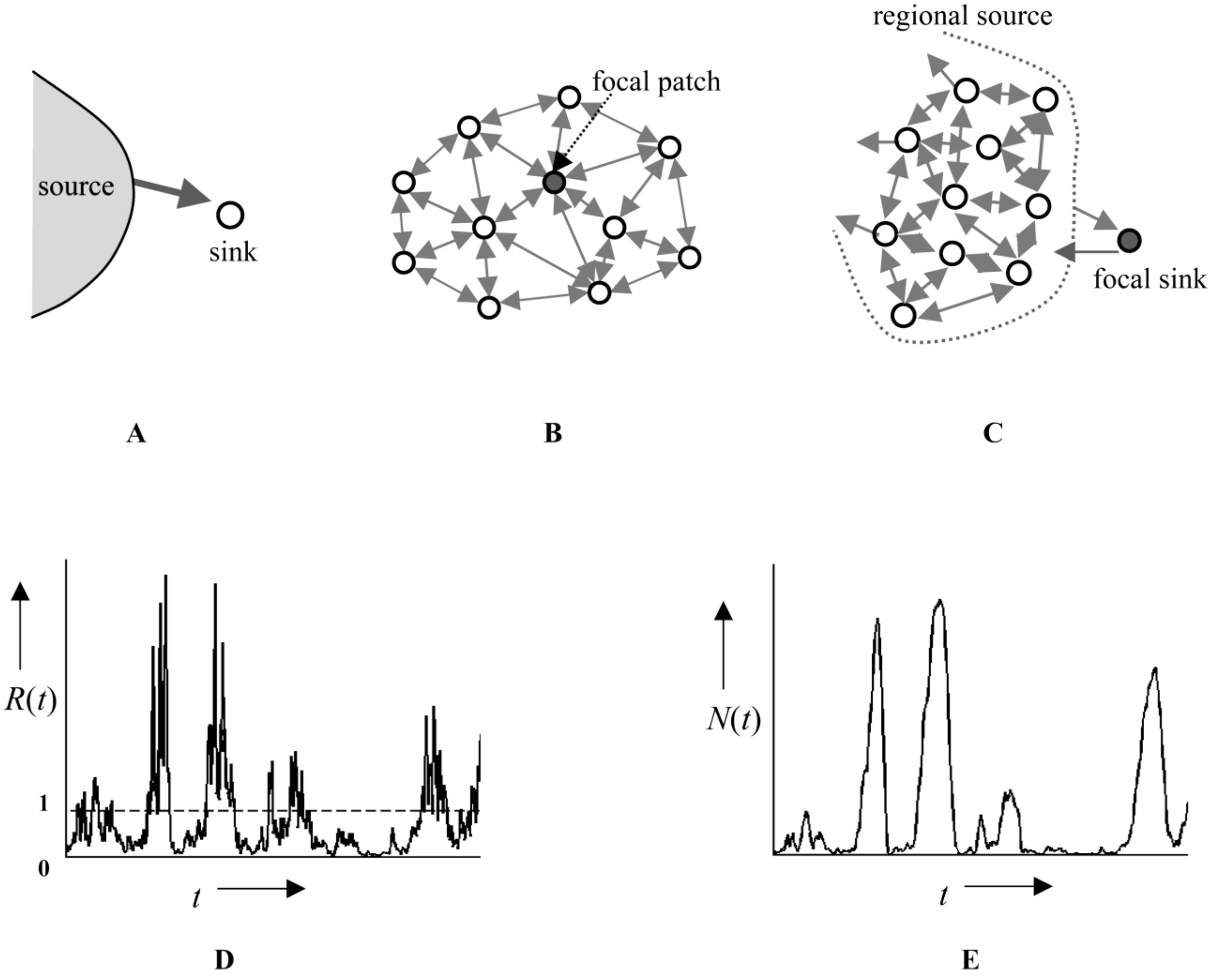

Figure 1: *A*, Diagram of a coupled source-sink system, with the arrow denoting the direction of the mass effect. *B*, Diagram of the Levins's classic metapopulation, with each circle representing a local population and bidirectional arrows denoting immigration and emigration. *C*, One can describe a sink metapopulation as a coupled source-sink system. *D*, Example of a positively autocorrelated $R(t)$ with $\mu_r = -1$, $\sigma_r = 1.2$, and $\rho_r = 0.9$, from equation (A1) in the online edition of the *American Naturalist*, for a source-sink system. *E*, Corresponding abundance time series $N(t)$ for the model given in the appendix in the online edition of the *American Naturalist* shows a clear correlation with the peaks of $R(t)$, giving $\mathrm{Cov}(R, N) > 0$.

1985), the time-averaged arithmetic mean abundance is given by

$$\overline{N} = \frac{\mathrm{Cov}\,(R, N) + \overline{I}}{1 - \overline{R}}, \qquad (2)$$

where $\mathrm{Cov}\,(R, N)$ is the temporal covariance between population size and growth rate in the sink (this expression is briefly mentioned in Holt et al. 2003 but not analyzed in detail). We use separate symbols to denote three different arithmetic means of a stochastic variable $X(t)$. The statistical mean is denoted by μ_X, a sample mean averaged over time is denoted by $\overline{X}$, as in equation (2), and a sample mean averaged over space is denoted by $\langle X \rangle$, as in equation (4).

We are interested in comparing constant sinks with otherwise similar but temporally variable sinks. Equilibrial abundance in a constant sink with constant immigration is $N^* = I/(1 - R)$. In a temporally varying environment, if the covariance between growth and abundance is 0 (i.e., if values of $R(t)$ are independent), the time-averaged abundance (eq. [2]) equals the equilibrial abundance observed in a constant environment where the immigration and growth rates are at their respective time-averaged arithmetic means. Thus, temporal variation alone does not affect the average abundance of the sink population.

However, a positive temporal autocorrelation in $R(t)$ often implies that $\mathrm{Cov}(R, N) > 0$, which from equation (2) produces a larger arithmetic mean abundance ($\overline{N}$) than expected in a similar, constant environment with the same average growth rate. Thus, positive autocorrelation in local growth rates inflates the average abundance of the sink population (see appendix in the online edition of the *American Naturalist* for additional details and a numerical example). By contrast, a negative covariance between growth rate and N (which could occur in cyclical environments where R alternates between high and low values) depresses average abundance in the sink. Density dependence in the sink could influence the covariance term in several different ways. If density dependence is negative (R declines with increasing N), the covariance can be reduced; by contrast, with positive density dependence (an Allee effect), it can shift in the opposite direction. In most of this article, we will assume that density dependence is negligible in sink environments.

In a positively autocorrelated environment, times of high abundance tend to occur during phases when growth rates are unusually high, leading to a positive growth-abundance covariance. This covariance boosts arithmetic mean abundance, as formally described by equation (2) (a numerical example demonstrating this covariance is shown in fig. 1*D*, 1*E*; Holt et al. [2003] explored this effect in detail in a continuous-time source-sink system). In source-sink landscapes, persistence arises simply because the source itself is assumed to persist. But what if the entire landscape consists of sink habitats, in which a species faces deterministic local and global extinction were dispersal cut off? In a classical metapopulation (schematically depicted in fig. 1*B*), a species occupies discrete habitable patches separated by an unsuitable matrix. Following local extinction, immigration permits recolonization of empty patches, provided that the species persists somewhere in the regional patch ensemble. In the idealized landscape of Levins's classic metapopulation (Levins 1969; Hanski 1999), local sites are either empty or occupied to near carrying capacity (Hanski 1999, p. 56), and immigrants can be drawn from any occupied patch to colonize empty patches. Local populations experience spatially and temporally uncorrelated extinctions, and colonization into empty patches due to emigration from occupied sites potentially sustains the regional population.

We conjectured that the inflationary effect of autocorrelated temporal variation in sink populations could potentially contribute to metapopulation persistence. Spatially uncorrelated extinctions can be an extreme limit of temporal variation in local growth rates (e.g., $R(t) = 0$ at some t guarantees local extinction). Spatially asynchronous fluctuations in growth rates can permit the persistence of ensembles of sink habitats linked by dispersal. For instance, Jansen and Yoshimura (1998; see also Holt 1997) show that between-patch dispersal can sustain a species in two coupled sink patches with independent fluctuations and no autocorrelation. A heuristic argument (Holt 1993) suggests that source-sink dynamics is implicitly embedded within the dynamics of metapopulations. Figure 1*C* reorders the metapopulation of figure 1*B* to portray the relationship between a single focal patch and the rest of the ensemble. Given a sufficiently large number of patches, removing the focal patch should have a negligible effect on the behavior of the ensemble. Yet, by contrast, removing the remainder of the ensemble should have a large effect on the dynamics of the focal patch. This asymmetry resembles that built into standard source-sink models. Viewed from the focal sink, all other patches collectively are a large regional source providing a stream of immigrants. If dispersal is sufficiently weak that patches are not synchronized and immigrants are drawn from a large number of patches, the rate of immigration might be relatively constant over a reasonable time horizon. Given an effectively constant input from an external source, positive autocorrelation in the growth rate of the focal patch should then increase its time-averaged abundance (Holt et al. 2003).

Because each patch in the metapopulation can in turn be viewed as the focal patch, we hypothesized that the local inflationary effect of autocorrelation could boost regional population size in the entire metapopulation and that the effect could even facilitate long-term persistence of the metapopulation via the enhancement of colonization rates due to increased local population sizes. However, this plausibility argument has several potential weaknesses. First, the model of sink dynamics leading to expression (2) ignores emigration. In general, emigration lowers local population size, weakening the magnitude of the inflationary effect; indeed, emigration can even cause extinction in source-sink systems (e.g., Holt 1985). Second, as shown in figure 1, sink populations with autocorrelated growth rates have a characteristic outbreak pattern, with sustained periods at low numbers. In more realistic models (e.g., with demographic stochasticity), this should elevate local extinction rates. Finally, the argument clearly fails if the metapopulation as a whole is crashing to extinction. In the next section, we show that despite these potential negative effects of positively autocorrelated temporal variation in local growth rates, the overall effect of such variation is to facilitate metapopulation persistence.

Basic Metapopulation Model

A habitat in which a species has a variable growth rate $R(t)$ with geometric mean $G_R < 1$ is a sink, and an isolated population there becomes extinct asymptotically with probability 1 (see appendix). In a metapopulation, local populations are linked by dispersal. The dynamics on the focal patch i is

$$N_i(t+1) = R_i(t)N_i(t) + I_i(t) - E_i(t), \tag{3}$$

where $I_i(t)$ and $E_i(t)$ are immigration to and emigration from patch i at time t (as in eq. [1]). Because local growth rates can vary through time and do so in different ways in different patches, our system has what Chesson (1978, 1981) refers to as local patch variability. Averaging over all patches cancels out the migration terms, leading to:

$$\langle N(t+1)\rangle = \langle R(t)N(t)\rangle = \langle R(t)\rangle\langle N(t)\rangle + \mathrm{Cov}\,(R_i(t), N_i(t)). \tag{4}$$

In the spatial average (denoted by angled brackets), each patch is weighted equally; the covariance is likewise taken over space. Defining a relative local density term $n_i(t) \equiv N_i(t)/\langle N(t)\rangle$, equation (4) becomes

$$\langle N(t+1)\rangle = [\langle R(t)\rangle + \mathrm{Cov}\,(R_i(t), n_i(t))]\langle N(t)\rangle \equiv \tilde{R}(t)\langle N(t)\rangle, \tag{5}$$

where $\tilde{R} \equiv \langle R\rangle + \mathrm{Cov}\,(R_i, n_i)$ is the mean per patch growth rate. (Chesson [2000] used a similar expression for the growth rate of a spatially distributed population but without discussing the potential contribution of localized temporal autocorrelation; see also Chesson et al. 2005.) The condition for metapopulation growth over one generation is

$$\tilde{R}(t) > 1. \tag{6}$$

For temporally uncorrelated $R_i(t)$ on each patch, the local growth-density covariance $\mathrm{Cov}\,(R_i, n_i)$ becomes 0, leaving

$$\tilde{R}(t) = \langle R(t)\rangle = \overline{R}, \tag{7}$$

where $\overline{R}$ denotes an arithmetic time average of $R(t)$. (The second equality above follows from the limiting assumption of a large spatially uncorrelated system under statistical stationarity, in which case both sample averages $\langle R\rangle$ and $\overline{R}$ approach the statistical average μ_R.) Thus, inequality (6) reduces to the following necessary condition for growth and possible asymptotic persistence, with no temporal autocorrelation:

$$\langle R\rangle > 1. \tag{8}$$

Metapopulation persistence in an array of coupled sink habitats therefore requires that the arithmetic mean growth rate across space exceeds unity. By contrast, for a positively autocorrelated $R_i(t)$, $\mathrm{Cov}\,(R_i, n_i)$ can be positive, potentially allowing persistence even if the arithmetic mean growth rate $\langle R\rangle < 1$. Positive autocorrelation in local growth rates thus enhances metapopulation growth even if the arithmetic mean growth rate across habitats is less than 1 (as assumed in most of our numerical examples; throughout the article, the geometric mean $G_R < 1$ on each patch).

Note that equation (4) is not affected by the absence of dispersal. Thus, there can be an increasing arithmetic mean abundance even though the metapopulation is becoming extinct. This is because from equation (7), population growth is determined by the arithmetic mean $\overline{R}$, whereas persistence in the absence of dispersal depends on the geometric mean G_R. Because $\overline{R} > G_R$ for any nonconstant sequence, it is possible to have $\overline{R} > 1$ even when $G_R < 1$ and therefore have a population whose expected value grows without bound even though it tends to extinction (Lewontin and Cohen 1969). For an ensemble of patches coupled by dispersal, however, persistence is no longer determined by G_R on each patch alone but is influenced by the cooperative effect of growth on all patches combined; the quantity $\langle R\rangle = \overline{R}$ reflects this aggregate growth.

In equation (2), the covariance is taken over a time series in abundance at a single site (the sink), whereas in equation (5), the covariance is taken in a snapshot over space, in an ensemble of patches that on average experience the same environments. Our conjecture that the inflationary effect observed in a single sink coupled to a persistent source sheds light on the persistence of an ensemble of coupled sinks in effect makes an ergodic assumption, relating a time average at a single site to a space average over many sites. A full analytic treatment of model (4) would require one to write down a closed-form expression for how the spatial covariance term changes over time. This is analytically challenging, and here we instead summarize extensive numerical studies.

In these studies, we represented the metapopulation as a grid of cells that can be connected with various dispersal scenarios. Each grid cell represents a patch with a local population described by equation (3). Each local population experiences a stochastic, lognormally distributed growth rate $R_i(t) = \exp[r_i(t)]$, where $i = 1, \ldots, L$ specifies a patch in a metapopulation of size L. Each $r_i(t)$ is a temporally autocorrelated Gaussian random process with statistical arithmetic mean μ_r, variance σ_r^2, and a correlation coefficient of ρ_r between successive generations of $r_i(t)$ (these parameters are assumed to be the same on all patches; see appendix for details on the implementation of $r_i(t)$). We chose $\mu_r < 0$ throughout the article, satisfying the sink condition $G_R = \exp(\mu_r) < 1$ locally on each patch. During each generation of the dynamics before dispersal, there is multiplicative growth within each patch i,

$$N_i'(t+1) = R_i(t)N_i(t)\exp\left[-\frac{N_i(t)}{K}\right]. \tag{9}$$

The exponential term introduces a form of local density dependence (the well-known Ricker model) preventing the population from increasing without bound. (Eq. [9] can be rewritten in terms of N normalized by K, so the value of K itself has little effect on the dynamics.) After local growth, each patch sends out a fraction m of its population (m denotes a constant, density-independent, per capita emigration rate) to a global pool, which is redistributed equally among patches. The abundance of patch i after dispersal is

$$N_i(t+1) = (1-m)N_i'(t+1) + \frac{m}{L}\sum_{j=1}^{L} N_j'(t+1). \tag{10}$$

We assume no mortality during dispersal. (Later, we briefly consider a number of realistic modifications of the model, including localized dispersal, spatial synchrony, mortality during dispersal, and an alternative form of density dependence.)

Because the growth rate is $R_i(t) = \exp[r_i(t)]$, where $r_i(t)$ is Gaussian, $R_i(t)$ is lognormally distributed with arithmetic mean μ_R, variance σ_R^2, and correlation ρ_R, which can be expressed in terms of the parameters of $r_i(t)$ as follows (see appendix):

$$\begin{aligned}\mu_R &= \exp\left(\mu_r + \frac{\sigma_r^2}{2}\right),\\ \sigma_R^2 &= \exp(2\mu_r + \sigma_r^2)[\exp(\sigma_r^2) - 1],\\ \rho_R &= \frac{\exp(\rho_r\sigma_r^2) - 1}{\exp(\sigma_r^2) - 1}.\end{aligned} \tag{11}$$

A positive correlation ρ_r for $r_i(t)$ gives $\rho_R > 0$, and uncorrelated $r_i(t)$ implies $\rho_R = 0$.

For temporally uncorrelated $r_i(t)$ and hence $R_i(t)$, and with $\langle R\rangle = \overline{R} = \mu_R$, equation (8) gives the necessary condition for persistence as $\exp(\mu_r + \sigma_r^2/2) > 1$, and thus $\sigma_r > (2|\mu_r|)^{1/2}$. Metapopulation persistence in our model requires that the temporal variability in $r(t)$ must exceed a threshold value; this will be referred to as the threshold standard deviation, σ_{th}. With no temporal correlation, therefore, persistence requires that

$$\sigma_{\text{th}} \geq \sqrt{2|\mu_r|}. \tag{12}$$

For positively autocorrelated $r_i(t)$, because persistence may occur with $\langle R\rangle < 1$, the required threshold variability is reduced.

Relation (12) predicts that the minimum threshold variability required for persistence should increase with $|\mu_r|$ (recall that $\mu_r < 0$). This is because with increasing $|\mu_r|$, the local sink conditions on each patch get harsher, and a higher magnitude of variability is needed to satisfy $r(t) > 0$ (and so $R(t) > 1$) sufficiently often to sustain the system.

The other prediction of this analysis is that the threshold temporal variability permitting persistence should decrease with positive temporal autocorrelation. The reason is essentially the same as sketched for the source-sink model earlier. For each local population, immigration from the ensemble permits the population to be maintained through runs of bad years. During runs of good years, the population can grow exponentially; an increase in temporal autocorrelation permits longer bouts of sustained local growth. If emigration does not drain away these local spurts of growth too rapidly, populations will grow at sites where $R_i(t)$ temporarily is high; this gives $\mathrm{Cov}(R_i, n_i) > 0$, a local inflationary effect that should facilitate overall metapopulation persistence. Greater autocorrelation should give a larger covariance between R and N and therefore should decrease the minimum value of $\langle R\rangle$ required for persistence, and thus it also should reduce the threshold standard deviation. We use two summary statistics to quantify the inflationary effect and metapopulation persistence (see appendix for details): probability of persistence P over a long span of time and arithmetic mean per patch abundance $\langle N\rangle$ averaged over many generations for a persisting metapopulation.

Results

Figure 2 presents simulation results showing the probability of persistence P and mean abundance $\langle N\rangle$ as functions of the standard deviation σ_r and autocorrelation ρ_r for $\mu_r = -0.1$ and globally uniform dispersal with high local retention ($m = 0.05$). In figure 2*A*, the probability of persistence jumps sharply from 0 to 1 across a threshold σ_{th} for all four values of correlation ρ_r. This is more prominent in figure 2*C*, where a greater range of ρ_r (from 0 to a high value of 0.95) is used. The threshold in this plot appears almost as a straight line lying diagonally on the (σ_r-ρ_r) plane, indicating a steady decrease of the threshold variability needed for metapopulation persistence with increasing autocorrelation. In figure 2*A* and 2*C*, the values of σ_r used in the simulations were integer multiples of 0.05, as were the ρ_r values in figure 2*C*. A finer resolution

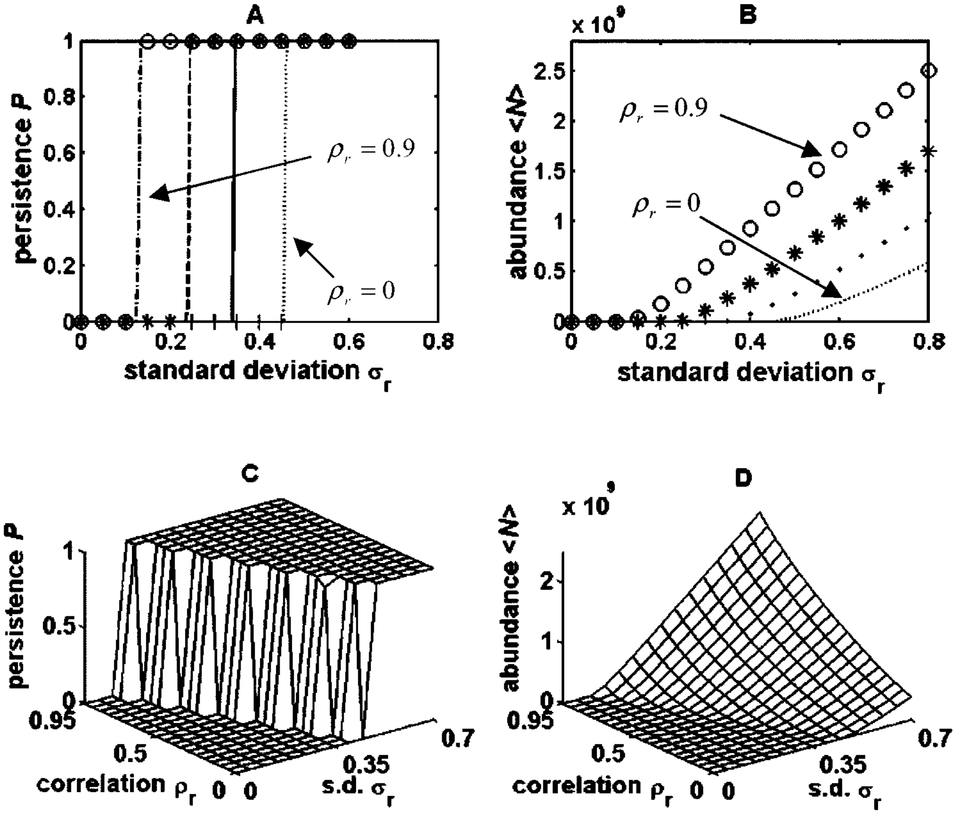

Figure 2: Inflation in a sink metapopulation. *A*, Persistence probability *P* versus standard deviation σ_r for four correlation values: $\rho_r = 0$ (*small dots*), 0.3 (*solid line*), 0.6 (*dashed line*), and 0.9 (*dash-dotted line*). Different line styles are used to highlight the sharp jump of *P* from 0 to 1 across the threshold σ_{th}. *B*, Arithmetic mean per patch abundance $\langle N \rangle$ versus σ_r for the same four ρ_r values as in *A* (*small dots*, *large dots*, *asterisks*, and *open circles*, respectively). *C*, Probability *P* plotted against both σ_r and ρ_r. *D*, $\langle N \rangle$ plotted against σ_r and ρ_r. For the simulation shown, $\mu_r = -0.1$, $m = 0.05$, there is globally uniform dispersal as in equation (10), and environments are spatially uncorrelated. (See appendix in the online edition of the *American Naturalist* for definitions of *P* and $\langle N \rangle$.)

of 0.005 was used for values of σ_r near the threshold in figure 2*A* and 2*B*. In almost all these cases, persistence was either 0 or 1, indicating a relatively sharp transition (this reflects the fact that we are using a continuous-state model, with a low threshold of abundance below which extinction is assumed). For persisting metapopulations, $\langle N \rangle$ increases with the magnitude of variability (σ_r). Moreover, the arithmetic mean abundance increases with ρ_r for any given value of variability permitting persistence. The shape of the surface in figure 2*D* bears a close resemblance to that of the comparable surface for the source-sink model shown in the appendix (fig. A1 in the online edition of the *American Naturalist*), demonstrating a qualitative correspondence of source-sink and metapopulation dynamics (as suggested by our heuristic argument given in "Temporal Variation and Sink Population Dynamics").

The dependence of σ_{th} (the minimum standard deviation of *r* required for persistence) on the autocorrelation coefficient ρ_r and $|\mu_r|$ is depicted in figure 3*A*. As predicted, σ_{th} decreases with ρ_r (almost linearly) for a given value of $|\mu_r|$ and also increases quite sharply with $|\mu_r|$ for any given ρ_r. The intercepts on the ordinate (the $\rho_r = 0$ line) give values of σ_{th} of 0.46, 1.12, and 1.68 for $\mu_r = -0.1$, -0.5, and -1, respectively, while relation (12) gives minimum threshold values of 0.45, 1.00, and 1.41. Thus, our results are close to the lower limit given in relation (12) for small $|\mu_r|$ but exceed the lower limit increasingly at higher $|\mu_r|$. Thus, the inequality $\overline{R} > 1$ alone does not guarantee persistence in uncorrelated environments (nor does it for an isolated sink, as in Lewontin and Cohen 1969). We cautiously conclude that the conditions for persistence derived above are necessary but not sufficient. Dispersal among coupled sink habitats may allow persistence in accord with relation (12) under certain circumstances (particularly for small $|\mu_r|$) but not always. The qualitative similarity of the shapes of the plots indicates

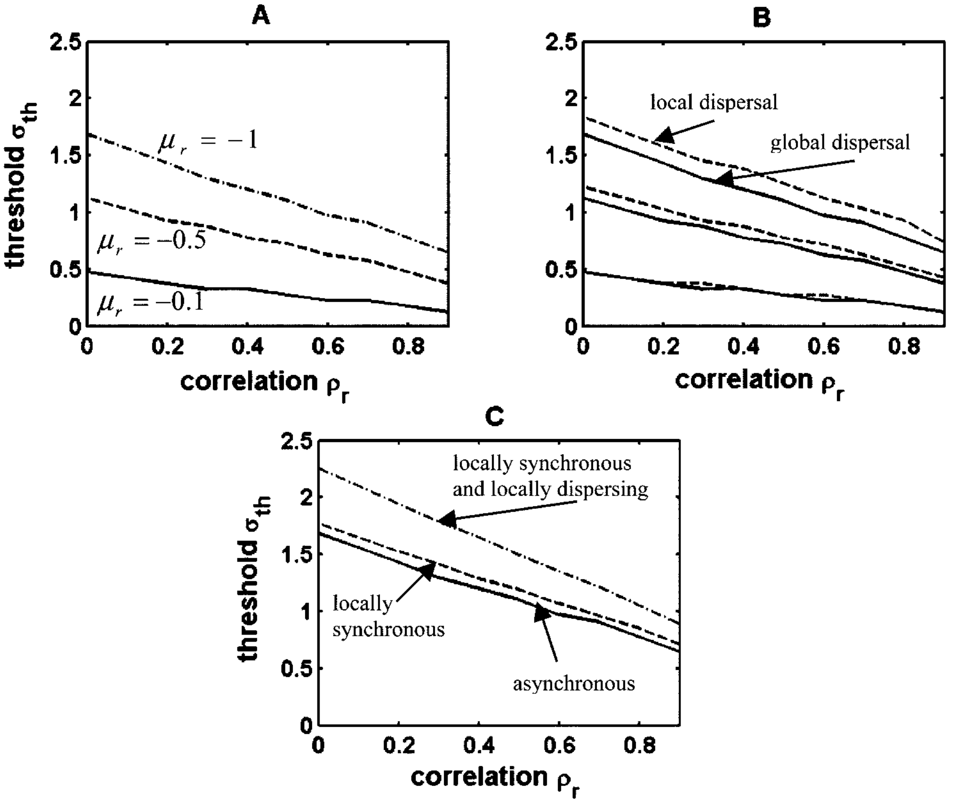

Figure 3: Examples of the inflationary effect, with some of the assumptions of figure 2 relaxed, illustrated with plots of the combinations of σ_{th} and ρ_r that separate parameters permitting metapopulation persistence versus extinction. *A*, Plots for three values of μ_r assuming global dispersal and no spatial correlation; other parameters are as in figure 2. For each line, parameters below the line entail extinction, and those above the line entail persistence. *B*, Comparing global (*solid lines*) and local (*dashed lines*) dispersal with $\alpha = 20$ (highly localized dispersal; see eq. [13]) for the same three μ_r values. *C*, Comparing spatial asynchrony and local synchrony generated with $\rho_s = 0.5$ (see appendix in the online edition of the *American Naturalist*) for $\mu_r = -1$ and global dispersal (other parameters as before). The combined effects of dispersal and patch synchrony are shown by comparing global and local dispersal in the presence of local synchrony. The dash-dotted line assumes moderate spatial synchrony ($\rho_s = 0.5$) and highly localized dispersal ($\alpha = 20$).

that these threshold properties are present even in very harsh sinks.

This twofold effect of the interplay of dispersal and autocorrelated growth rates on the dynamics, namely, the lowering of the threshold variability that permits persistence and the increase of arithmetic mean per patch abundance, is what we refer to as the inflationary effect of autocorrelated variation in a sink metapopulation.

Metapopulation dynamics is significantly affected by the magnitude of dispersal (Hill et al. 2002), which in our model is the per capita emigration rate m. The results of figures 2 and 3*A* assumed a low value of m ($=0.05$), equivalent to high philopatry. With increasing m, the patches become synchronized; complete mixing occurs if $m = 1$. The qualitative effect of mixing on metapopulation persistence can be seen by recalling the expression for the mean per patch growth rate $\tilde{R} \equiv \langle R \rangle + \mathrm{Cov}(R_i, n_i) = \overline{R} + \rho_{Rn}\sigma_R\sigma_n$, where ρ_{Rn} is the cross-correlation coefficient between $R_i(t)$ and $n_i(t)$ and σ_R^2 and σ_n^2 are their variances. For $m = 0$, there is no dispersal, and so $n_i(t)$ and hence σ_n^2 both vanish asymptotically; for $m = 1$, populations completely mix at every time step and hence $\rho_{Rn} = 0$. Therefore, at both extremes of m, we have $\mathrm{Cov}(R_i, n_i) = 0$ irrespective of the temporal autocorrelation in $R_i(t)$; there is no local inflationary impact of autocorrelation, and the metapopulation becomes extinct asymptotically if $\overline{R} < 1$. Thus, we would expect both the probability of persistence and the arithmetic mean abundance to peak at an intermediate range of m and to go to 0 at both low and high values for m when the average growth rate is below 1 (see also Nachman 2000). Numerical examples are shown in figure 4*A*–4*C* for $\overline{R} < 1$. The probability of persistence P and the arithmetic mean per patch abundance $\langle N \rangle$ exhibit maxima at intermediate

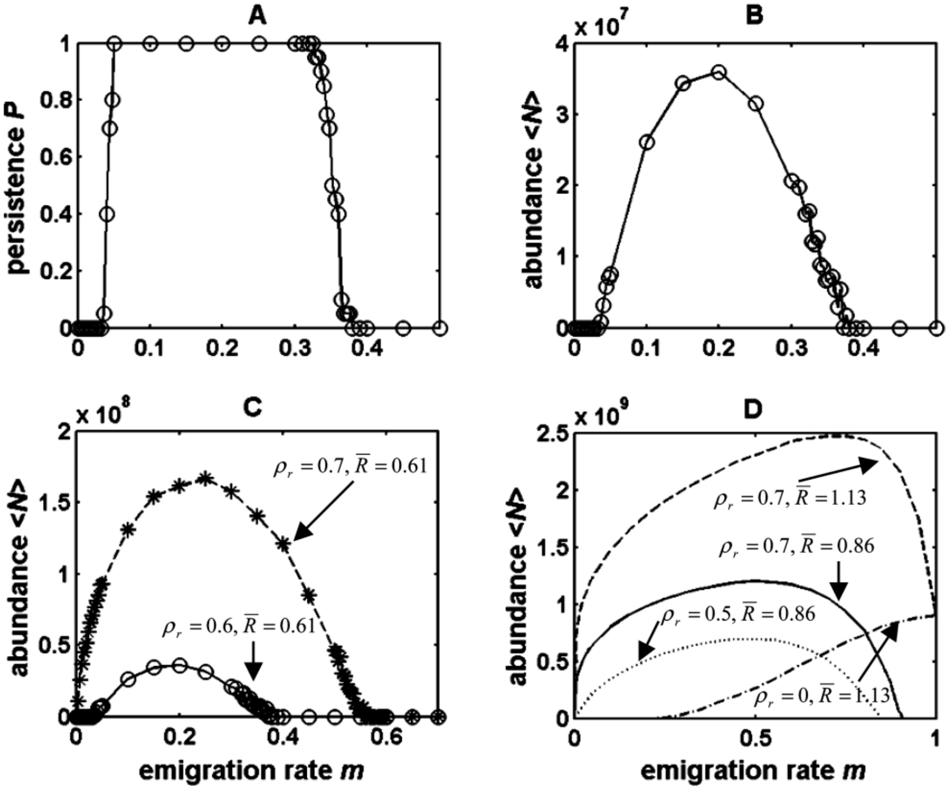

Figure 4: *A* and *B* show the probability of persistence *P* and arithmetic mean per patch abundance $\langle N \rangle$ plotted against per capita emigration rate *m* for $\mu_r = -1$, $\sigma_r = 1$, $\rho_r = 0.6$, and globally uniform dispersal and spatial asynchrony. *C*, $\langle N \rangle$ versus *m* for $\rho_r = 0.6$ (same as *B*) and $\rho_r = 0.7$. From equation (11), $\langle R \rangle = \overline{R} = 0.61$. *D*, Autocorrelation increases the range of dispersal permitting persistence, for both $\overline{R} < 1$ and $\overline{R} > 1$, and can have large effects on average abundance even when $\overline{R} > 1$. For persistence, the metapopulation survived for 20,000 time steps. The calculations of $\langle N \rangle$ use the average abundance of populations from 10,000 to 20,000 generations for populations that survived to the end of the simulation.

values of *m*. In figure 4*C*, $\langle N \rangle$ is plotted for two different autocorrelation values; the increased magnitude of the inflationary effect at higher correlation increases the range of *m* permitting persistence (indicated by a positive $\langle N \rangle$ over a broader range of *m*; these abundances are calculated only for persistent populations, so the intersection of the humps with the *X*-axis describes the range of *m* allowing persistence for a given autocorrelation). Figure 4*D* combines the results of figure 4*C* (drawn with slightly different parameters to highlight differences) and includes examples for $\overline{R} > 1$, with and without autocorrelation. If the arithmetic mean growth rate exceeds 1, the metapopulation can persist even with complete mixing, $m = 1$ (we are assuming a geometric mean growth rate less than 1). For uncorrelated variation ($\rho_r = 0$) and $\overline{R} > 1$, persistence requires substantial mixing (recall that if the geometric mean is less than 1, isolated populations become extinct). With autocorrelation, even a slight degree of mixing in this example ensures metapopulation persistence and dramatically increases arithmetic mean abundance. The example in figure 4*D* highlights the potential importance of positive autocorrelation in enhancing metapopulation persistence and abundance even in systems where the average growth rate exceeds unity so that autocorrelation is not an absolute requirement for persistence.

Generalizations and Extensions

The above metapopulation model makes many simplifying assumptions, including, first, individuals disperse homogeneously across the entire metapopulation; second, there is no spatial correlation among patches, and all patches are statistically identical; and third, population size is represented as a continuous variable rather than discrete integers, so there is no demographic stochasticity. We now relax these assumptions.

Localized Dispersal

The basic model assumes uniform global dispersal (eq. [10]). In reality, however, dispersal is localized. An inverse power-law dispersal kernel has been suggested to approximate many natural dispersal scenarios (Levin et al. 2003). We modified the basic model by incorporating the following inverse power-law expression for dispersal:

$$N_i(t+1) = (1-m)N_i'(t+1) + \frac{m}{\sum_{k\neq i} 1/d_{ik}^{\alpha}}\left[\sum_{j\neq i}\frac{N_j'(t+1)}{d_{ij}^{\alpha}}\right] \qquad (13)$$

where d_{ij} denotes the distance between the *i*th and *j*th patches in the metapopulation and the exponent α is an inverse measure of dispersal range. High and low α, respectively, correspond to short- and long-range dispersal; $\alpha = 0$ implies globally uniform dispersal (approximating eq. [10] with L replaced by $L-1$ and the sum excluding the focal patch i because in eq. [13], dispersers arrive from all other patches [the difference between the two is negligible for a large metapopulation]). We also considered a neighborhood form of dispersal among clusters of four and eight neighboring patches; in these examples, equation (13) takes the form

$$N_i(t+1) = (1-m)N_i'(t+1) + \frac{m}{n}\sum_{j} N_j'(t+1), \qquad (14)$$

where n is the neighborhood size ($n = 4, 8$) and j runs over neighboring patch indexes.

Local dispersal should weaken the inflationary effect presented in figure 3*A* (which assumes global dispersal) because now immigrants are drawn from a smaller pool of fluctuating populations. Figure 3*B* compares global and local dispersal; the plots of figure 3*A* are overlaid with similar plots for $\alpha = 20$, corresponding to a highly localized dispersal confined almost entirely to nearest neighbors. The threshold is larger with a locally dispersing population for all values of autocorrelation ρ_r, particularly at higher $|\mu_r|$ (i.e., harsher local environments). Given local dispersal, immigrants arrive only from neighboring patches, so the favorable effect of a large local population size sustaining other patches with low growth rates is restricted to nearby patches rather than distributed over all patches. The difference, however, decreases with decreasing $|\mu_r|$, and when $\mu_r = -0.1$, the plots appear to coincide. The reason is that in a weak sink, little immigration is needed to sustain a local population in periods of less favorable growth. The two sets of plots have similar shapes, implying that the inflationary effect with respect to persistence is qualitatively robust to changes in the dispersal range. Localized dispersal also influences the patterns shown in figure 4 by reducing the range of m that permits persistence and lowering the arithmetic mean abundance of the persisting metapopulation (results not shown).

Spatially Synchronous Environments

In the model described above, the growth rates $R_i(t)$ are assumed to be spatially uncorrelated. This is a useful theoretical abstraction but rarely describes reality. Many abiotic and biotic factors, including regional climate and broadscale disturbance, can create synchrony by coupling the environments of neighboring patches. To examine the impact of such synchronizing mechanisms on the inflationary effect, we incorporate a spatial correlation in $r_i(t)$ that decays with distance d_{ik} between patches; the correlation coefficient is $\rho_{\mathrm{s}}^{d_{ik}}$, where ρ_{s} is the spatial correlation coefficient between adjacent patches (see appendix for details). With $\rho_{\mathrm{s}} = 0$, this model reduces to the familiar spatially uncorrelated and temporally autocorrelated model above. By contrast, with $\rho_{\mathrm{s}} = 1$, the growth rates $r_i(t)$ across all patches become globally synchronized to a single rate $r(t)$ fluctuating in time with autocorrelation ρ_r and variance σ_r^2, in effect reducing the entire metapopulation to a single large sink population that eventually becomes extinct (because there is no net immigration from external sources).

The effect of a moderately strong local synchrony ($\rho_{\mathrm{s}} = 0.5$) on the persistence threshold is shown in figure 3*C* for a globally dispersing metapopulation along with a similar but spatially asynchronous case. Spatial synchrony increases the threshold σ_{th} required for persistence for all values of correlation ρ_r; the difference between the two plots is, however, modest. With locally synchronous dynamics, a number of neighboring patches experience similar growth rates. In effect, for a given finite grid size, introducing spatial synchrony makes it less likely that there will be some patches where the local growth rate exceeds unity in any generation. Nonetheless, the contribution of local "inflation" to metapopulation persistence is qualitatively robust to local synchrony.

As noted above (fig. 3*B*), localized dispersal inhibits the inflationary effect by limiting immigration. Combining local synchrony with local dispersal weakens the persistence effect of positive autocorrelation (see fig. 3*C*) but does not eliminate it. Compared with global dispersal and no spatial correlation, either local dispersal or spatial correlation reduces the maximum growth rate of patches providing immigrants to a typical patch and thus weakens the inflationary effect. With local dispersal, this is because fewer patches provide immigrants to each patch. With spatial correlation and global dispersal in a finite lattice, there is

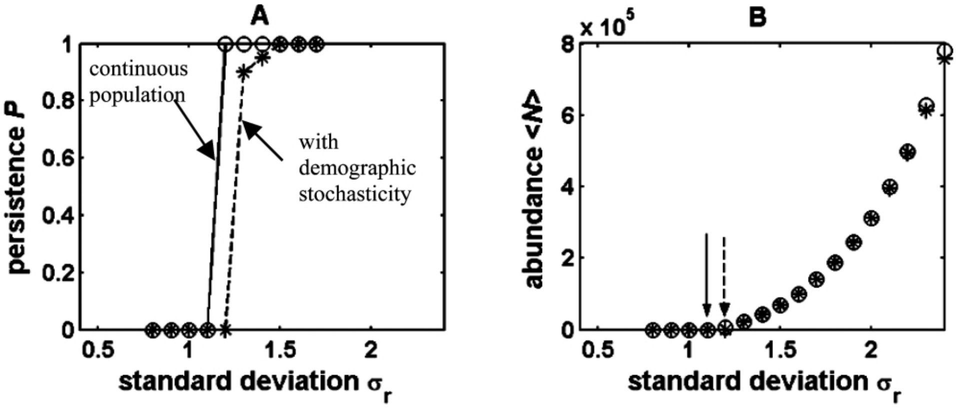

Figure 5: *A* and *B* show the effect of demographic stochasticity on inflation by plotting persistence P and abundance $\langle N\rangle$ versus the standard deviation σ_r for a continuous population (*open circles*, *solid line*) and integer population with demographic stochasticity (*asterisks*, *dashed line*), both with initial random seeding of 50% of patches and eight-neighbor dispersal. The arrows in *B* indicate threshold values σ_{th} for $\langle N\rangle > 0$ in the two cases, which are the same as for $p > 0$ in *A*. Other parameters are $\mu_r = -1$, $\rho_r = 0.6$, $K = 10^6$, $m = 0.05$.

a reduction in the range of growth rates likely to be observed in any generation. For the example shown ($\rho_s = 0.5$), even though there is significant correlation between adjacent patches, across the landscape the average correlation between patches is less than 0.1. Thus, the effect of local synchrony with global dispersal is modest. With both local dispersal and spatial correlation, however, each patch receives immigrants mostly from its nearest neighbors, with which it is also more highly correlated. The effect of spatial correlation on reducing inflation is magnified with local dispersal (fig. 3*C*). It should be noted, however, that there can be a marked effect of autocorrelation on persistence even with local dispersal in spatially synchronized environments (as in the example of fig. 3). Other studies have also noted interesting, nonintuitive interactions between the spatial scale of dispersal and spatial correlation in generating population synchrony (Kendall et al. 2000; Engen et al. 2002).

Demographic Stochasticity

The deterministic processes of growth (eq. [9]) and localized dispersal (eqq. [13], [14]) involve continuous population sizes that can become arbitrarily small without ever becoming extinct (“nano-individuals”; see Wilson et al. 1998). This assumption of continuity works well for large populations but may not be reasonable in sink environments where populations may approach very low densities. In our simulations, most local populations remain bounded well away from 0 (see fig. A2 in the online edition of the *American Naturalist* for an example). Nonetheless, it is important to consider the effects of demographic stochasticity. We examined a model with growth and dispersal analogous to equations (9) and (14) but incorporating demographic stochasticity with discrete individuals, for which extinction occurs naturally whenever $N_i(t) = 0$. In this model, the number of individuals after reproduction is a Poisson random variable with arithmetic mean given by the right-hand side of equation (9). Each newborn migrates randomly from its natal patch to one of n neighboring patches with equal probability m/n. So now immigration is also stochastic and by chance can be 0 for any given patch. Figure 5*A* and 5*B*, respectively, compares persistence and mean abundance plots for continuous and integer populations. Random occupancy of 50% of patches (with 10 individuals each) is the initial condition. The plots exhibit a good agreement between the two models, except for a slightly higher threshold for the individual-based model. As expected, incorporating demographic stochasticity makes extinction more likely, but it does not wash out the predicted impact of temporal autocorrelation on metapopulation persistence. With demographic stochasticity, there is also a dependence on initial conditions. If initially all individuals are confined to a single patch, many introductions will rapidly become extinct before they have a chance to exploit transient conditions, spread, and become established. Our results thus bear more on persistence of established populations than on the conditions for initial establishment.

We have also considered a number of additional extensions of the models and here just note the effects without belaboring the details. If instead of the Ricker model one assumes “ceiling” density dependence, where each local population is limited by an integer carrying capacity K, with no density dependence below K, and experiences demographic stochasticity, then as expected, extinction becomes more likely as K is reduced. Nonetheless, an increase in autocorrelation does reduce the amount of temporal variation required to sustain the metapopulation and permits population persistence when $\overline{R} < 1$. Moreover, at larger K, persistence becomes possible with lower magnitudes of variation and autocorrelation.

We explored the effect of introducing mortality due to dispersal by modifying equation (10) for global dispersal to reduce the number of emigrants surviving to enter other patches. Moderate mortality (e.g., up to 50%) reduces the range of m over which the metapopulation persists and decreases mean abundance compared to the patterns shown in figure 4*C*, but the unimodal pattern is still present with appreciably large $\langle N \rangle$. We also considered a fractal pattern of patch distribution separated by an inhospitable matrix of unsuitable patches that act as dispersal barriers (Saupe 1988). The inflationary effect is fairly robust to changing patch connectivity. Finally, we have assumed that individuals move at a constant, fixed rate. If instead movement rates are labile and individuals are more likely to leave patches where fitness is relatively low, this will enhance the persistence of the metapopulation. Such a conditional dispersal strategy makes sense only if there is a degree of predictability in local growth rates, measured by the positive autocorrelation. The inflationary effect of autocorrelated temporal variation on population persistence and abundance should thus be enhanced if individuals have flexible and adaptively sensible movement rules. Overall, we conclude that the impact of positive temporal autocorrelation on facilitating metapopulation persistence and abundance in ensembles of sink habitats is robust to a wide range of modifications of the basic model.

Discussion

The synergistic interplay of temporal variability and spatial fluxes in ecological systems is a topic of increasing interest at all levels of ecological organization (Sears et al. 2004). We conjectured that the inflationary effect of temporally correlated variation in sink populations sustained by immigration from a source, demonstrated by Gonzalez and Holt (2002) and Holt et al. (2003) and given by expression (2) above, would generalize to ensembles of patches, all of which are on average sink habitats. The results presented here show that this conjecture holds. Given temporal variability and positive temporal autocorrelation in local growth rates, moderate rates of dispersal can enhance the ability of a sink metapopulation to persist; moreover, given persistence, temporal autocorrelation can inflate metapopulation abundance. This phenomenon is qualitatively reasonably robust to a variety of realistic factors including localized dispersal, spatial synchrony in patch conditions, demographic stochasticity, habitat fragmentation (creating dispersal barriers), and a moderate ceiling on local density (although these factors reduce the quantitative impact of the predicted effect).

One intuitive way to understand why positive temporal autocorrelation can facilitate the persistence of a metapopulation of coupled sinks goes as follows. We have seen that an increase in autocorrelation generally decreases the magnitude of temporal variation required for persistence, particularly for weak sinks where the rate of decline in bad years is slow, when all patches have growth rates drawn from the same statistical distribution. In the limit of an autocorrelation coefficient of 1, it is as if the initial condition of the landscape were fixed in time. If, by chance, some sites have an initially positive growth rate, they will continue in this favorable state indefinitely. If migration is sufficiently weak, this will not preclude the persistence of the species in these initially lucky patches with positive growth rates, but it will permit maintenance of the species in other patches permanently fixed in a sink state with negative local growth rates. In other words, as the autocorrelation coefficient gets larger, in effect the dynamic landscape increasingly converges on the idealized scenario of figure 1*A*, where permanent sources exist and permit the indefinite presence of a species in permanent sink habitats. Our results show that this source-sink effect contributes to persistence of a metapopulation in dynamic landscapes where patch qualities are not spatially fixed through time but instead are predictable over a time horizon defined by the autocorrelation coefficient.

We would not wish to push the proposition that the inflationary effect all on its own will be a major determinant of species persistence in patchy or fragmented landscapes. In many systems, spatial heterogeneity is key to persistence (Holt 1993), and permanent source habitats may be required for long-term species persistence (Harrison and Taylor 1997). Nonetheless, the inflationary effect arising from localized temporal autocorrelations could help sustain larger population sizes over the landscape.

In classical metapopulation dynamics, patches are either empty or occupied at carrying capacity. There has been a growing appreciation of the need to consider within-patch population dynamics when analyzing the regional dynamics of metapopulations (Hanski 1999; Harding and McNamara 2002; Hanski and Gaggiotti 2004). Our results provide a particular example of this general insight. The inflationary effect arises because with limited dispersal, a local population can grow and exploit transient runs of favorable conditions even in environments that on average do not permit long-term persistence without recurrent immigration. High rates of dispersal lead to high rates of emigration, preventing local populations from being able to exploit localized transient runs of good conditions. Other authors (Earn et al. 2000; Cazelles et al. 2001; Liebhold et al. 2004) have explored how high dispersal can lead to coherent oscillations among local populations in a metapopulation so that global excursions to low numbers and extinction become possible. This effect differs from and complements the inflationary effect explored here.

Many mechanisms can potentially lead to local, positive temporal autocorrelations in growth rates. At the most general level, ecological "memory" that is spatially localized (Hendry and McGlade 1995) can lead to a positive autocorrelation in local growth rates. Consider the following very simple model for how ecological memory in a limiting resource can generate positive autocorrelation in the dynamics of its consumer. A resource-limited organism with discrete generations is assumed to have a birth rate that increases linearly with the abundance $D(t)$ of an abiotic resource (say births $= bD(t)$), such as soil water or a detrital pool, and a constant survival rate s after birth. The net growth rate is thus $sbD(t)$. A constant fraction $1 - k$ of the resource decays or disappears per generation, and the resource is input at a rate of $i(t)$ (assumed positive), where $i(t)$ is described by an independent and identically distributed stochastic process in time and space. The resource dynamics is described by $D(t+1) = kD(t) + i(t)$. Even though there is no autocorrelation in the input term, the carryover in resource abundance between successive time steps implies that $D(t)$ is positively autocorrelated at each site. Hence, the local population growth rate will also be positively autocorrelated, with no spatial synchrony. Similarly, if the dynamics of a focal species when rare is strongly influenced by interactions with another species, this can generate a local temporal correlation in the focal species' growth rate. Roughgarden (1975) noted that a species with discrete generations and logistic growth experiencing uncorrelated stochastic variation in its carrying capacity can show a positive correlation in its abundance N' over time; here, ecological memory is expressed in population size. If this species is a dominant competitor or predator and the negative effect on the growth rate of an inferior competitor or prey species scales with N' (as in Lotka-Volterra models), the inferior competitor or prey species will experience a positively autocorrelated time series in a component of its growth rate.

The inflationary effect may be implicitly embedded within the mechanisms operating in familiar metapopulation models. For instance, consider a system in which two plant species coexist because of a competition-colonization trade-off. For simplicity, assume the inferior competitor is a superior colonizer into empty patches but has no effect on the superior competitor. Given asymmetric competition (Tilman 1994), spatial gaps within colonies of the dominant competitor caused by extinction in effect constitute transient favorable patches (patches with high growth rates, permitted by absence of the superior species) for the weaker species. Because of its assumed poor colonizing ability, the dominant species takes longer to reoccupy gaps following local extinction. The time elapsing between extinction and recolonization by the superior species provides a period with a positive expected growth rate for the inferior species. With the dominant species present, the same patch has a negative growth rate for the inferior species. Thus, in a sense, the dynamics of the superior species creates a positively autocorrelated environment for the inferior species. Indeed, gap dynamics governed by a disturbance-recovery-type mechanism in model systems is known to generate interesting correlation patterns in time and space (Guichard et al. 2003), significantly influencing the persistence and abundance patterns of successional communities in these gaps (Roy et al. 2004). B. Bolker (personal communication) has suggested that the inflationary effect may be implicit in the concept of temporal successional niches, where species persist because of exploitation of transient phases of good conditions (e.g., after disturbance removes a superior species).

As another example of spatially mediated coexistence that may involve the inflationary effect, in a coupled map lattice model of apparent competition involving host-parasitoid interactions with global dispersal, the inferior competitor host in a cluster of locally synchronous patches is rescued from extinction by immigration from other out-of-phase clusters (King and Hastings 2003). These authors note, as do we (fig. 1; see also Holt 1993, p. 85), that in an ensemble of patches, from the perspective of any single patch, the remainder of the ensemble can be viewed as providing a source of recurrent immigration. The particular mechanism they examine, which involves the emergence of phase differences among patches due to localized host-parasitoid interactions, differs in detail from the one we have examined but is similar in that it involves asynchronous dynamics across space. In our system, asynchronous dynamics and autocorrelated growth rates are driven by external factors; in the metapopulation system explored by King and Hastings (2003), asynchronous dynamics emerges internally from localized, unstable host-parasitoid interactions, and autocorrelated growth rates arise from localized population growth. An important task for our future work is to examine explicitly the influence of temporal autocorrelation on the coexistence of multiple interacting species.

We might note a practical implication for the design of surveys meant to facilitate species conservation. In the examples of figure 4*C*, for instance, the realized arithmetic mean growth rate per generation across space is 0.61. A laborious field study documenting an average of local growth rates across space, estimated from local births and deaths, would thus suggest that the species is experiencing a precipitous decline in numbers (by more than 60% over two generations). Yet in our example, this species with moderate movement rates can actually persist at high numbers because of the inflationary effect resulting from autocorrelation in local population growth rates. What is needed to apply our theoretical ideas to natural populations is not a single snapshot of population growth rates but instead spatially structured sampling protocols, with repeated samples at the same locations, permitting an assessment of the magnitude of temporal autocorrelation in local growth rates.

One effect of positive temporal autocorrelation in our models is that total population size is maximized at intermediate dispersal rates (see fig. 4). Similar patterns arise in a broad spectrum of models with unstable population dynamics. For instance, Holt (1983*a*, 1983*b*) showed that an intermediate immigration rate could lead to the greatest population size for a persistent population with unstable dynamics (as a result of strong density dependence). Nonmonotonic effects of dispersal rate on abundance can arise without local extinctions in arrays of identical patches with locally unstable dynamics, perturbed by random variation in local growth rates (Holt 1993; Ives et al. 2004) and in classical metapopulation models (Hanski and Zhang 1993; Hanski 1999). These models make many different assumptions (e.g., about density dependence), yet all point to the same conclusion that increased dispersal rates can at times depress total population size in a patchy and temporally varying environment.

We have focused on the impact of positive temporal autocorrelation in growth rates on increasing the likelihood of metapopulation persistence. In some circumstances, one might instead observe negative autocorrelation in local growth rates (e.g., for a prey species if a generalist predator exhibits strong generation cycles). This makes it more difficult for a metapopulation to persist even in environments where the arithmetic mean growth rate is greater than unity (details not shown). Finally, there is an increasing concern with how anthropogenic forces are changing climatic regimes (Walther et al. 2002; Visser et al. 2004). Most attention has focused on how mean climatic variables can alter because of increases in atmospheric carbon dioxide. Our results suggest that one should also consider potential shifts in the structure of temporal variation during climate change. If a metapopulation persists because a dispersing species can exploit transient pulses of locally favorable conditions, a reduction in the positive autocorrelation of the environment can potentially lead to catastrophic declines in abundance and even extinction. Moreover, consistent with other studies (e.g., Earn et al. 2000), our results show that increases in the rate of movement may not always facilitate the persistence of a species in a patchy and temporally variable landscape. Increasing landscape connectivity through dispersal is not a panacea for preserving species facing extinction in our increasingly patchy and temporally uncertain world.

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