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# Impacts of environmental variability in open populations and communities: “inflation” in sink environments

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## Abstract

Ecological communities are typically open to the immigration and emigration of individuals, and also variable through time. In this paper we argue that interesting and potentially important effects arise when one splices together spatial fluxes and temporal variability. The particular system we examine is a sink habitat, where a species faces deterministic extinction but is rescued by recurrent immigration. We have shown, using a simple extension of the canonical exponential growth model in a time-varying environment, that variation “inflates” the average abundance of sink populations. We can analytically quantify the magnitude of this effect in several special cases (square-wave temporal variation and Gaussian stochastic variation). The inflationary effect can be large in “intermittent” sinks (where there are periods with positive growth), and when temporal variation is strongly autocorrelated. The effect appears to be robust to incorporation of demographic stochasticity (due to discrete birth–death–immigration processes), and to direct density dependence. With discrete generations, however, one can observe a wide range of effects of temporal variation, including depression as well as inflation. We argue that the inflationary effect of temporal variation in sink habitats can have important implications for community structure, because it can increase the average abundance (and hence local impacts) of species that on average are being excluded from a local community. We illustrate the latter effect using a familiar model of exploitative competition for a single limiting resource. We demonstrate that temporal variation can reverse local competitive dominance, even to the extent of allowing an inferior competitor maintained by immigration to exclude a competing species that would be locally superior in a constant environment.

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## 1. Introduction

Most experimental and observational studies in ecology are conducted at relatively modest spatial and temporal scales (Kareiva and Andersen, 1988). Yet ecologists are becoming increasingly aware that the structure and dynamics of local populations and communities may reflect processes operating at large spatial scales over long periods of time (e.g. Cornell and Lawton, 1992; Karlson and Cornell, 2002; Ricklefs and Schluter, 1993). From a mechanistic perspective, local communities are coupled to broader landscapes via fluxes of individuals and materials. In many circumstances, such fluxes can be strong and asymmetrical (Polis et al., 1997; Power and Rainey, 2000), with

consequences ramifying through many levels of ecological organization. For a single species occupying an array of heterogeneous patches, flows of individuals from high-quality habitats can sustain populations in low-quality habitats, creating a “source–sink” population structure (Holt, 1985; Pulliam, 1988; Pulliam and Danielson, 1991; Brawn and Robinson, 1996; Ritchie, 1997; With and King, 2001). At the community level, such flows permit species sustained in one habitat to persist locally in other habitats, despite a trend towards exclusion from resident species due to negative interactions such as competition and predation. This “mass effect” can enrich local assemblages in heterogeneous landscapes (Shmida and Wilson, 1985) or stabilize complex communities (Huxel and McCann, 1998). At the level of entire ecosystems, system openness has profound consequences for ecosystem functioning and the relationship of biodiversity to ecosystem processes

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(Gonzalez and Chanuton, 2002; Holt and Loreau, 2002; Polis et al., in press).

These spatial fluxes are not constant through time, nor do they occur in a world that is otherwise fixed. Ecologists have long recognized the potential importance of temporal variation in the maintenance of species diversity (Chesson and Huntly, 1993). Despite an appreciation of the significance of spatial heterogeneity for species coexistence (e.g., Brown, 2000), there has been remarkably little attention given to the consequences of overlaying spatial fluxes and temporal variability (but see Chesson, 2000). In this paper, we use several simple models to argue that the impact of spatial fluxes on local populations and communities can at times be greatly magnified by temporal variation in the local environment. As we shall see, temporal variation can substantially enhance the “mass effect.” This consequence of temporal variation can in turn constrain species richness, by making it more difficult for species specialized to particular habitats to persist in the face of immigration by other species.

The most important factors of the environment for many species are often the abundances and activity levels of other species. Variation in abundance (which is the norm, not the exception in natural systems (Strong, 1986; Pimm and Redfearn, 1988; Ives, 1995; Inchausti and Halley, 2001)) can arise from direct forcing of the physical environment (Andrewartha and Birch, 1954; Lawton, 1995; Hawkins and Holyoak, 1998; Sagarin et al., 1999), from intrinsic sources of instability, or from the interplay of extrinsic forces and nonlinear population responses (e.g., Kaitala et al., 1997; Dixon et al., 1999; Blarer and Doebeli, 1999; Pascual et al., 2000). In multispecies food webs, temporal variation in the strength of interaction between any given pair of species can be generated by fluctuations in the abundances of other community members (Berlow, 1999) or changes in the magnitude of per capita effects (Witman and Grange, 1998; Post et al., 1999; Sanford, 1999) including adaptive responses to a variable environment (Abrams, 1997) and changes in community composition (Bengtsson et al., 1997).

One aspect of temporal variation that may be particularly significant for ecological dynamics is its autocorrelation structure. Fluctuations of many physical variables (e.g., rainfall) are positively autocorrelated (Steele, 1985; Schoener, 1985; Wigley et al., 1998), as are fluctuations of both natural populations (Arino and Pimm, 1995; Halley, 1996; Gillman and Dodd, 1998; Inchausti and Halley, 2001) and populations in laboratory microcosms (Petchey, 2000). Although there are a considerable number of theoretical studies of the impact of such autocorrelation on different aspects of population and community dynamics (e.g., Kaitala et al., 1997; Petchey et al., 1997; Ripa and Lundberg, 1996; Ripa et al., 1998), little attention has been given to

the consequences of the interplay of autocorrelated temporal variability and spatial heterogeneity.

We start by examining the dynamics of a sink population, maintained by recurrent immigration from a source habitat. After presenting an argument suggesting that temporal variation in local growth rates tends to increase the average abundance of sink populations, we examine in detail a special case that permits a closed-form analytic solution (square-wave variation). We show that the “inflationary” impact of temporal variation on abundance in a sink habitat in this special case is robust to the incorporation of demographic stochasticity. We then examine a model with stochastic, autocorrelated variation in growth rates, with and without density dependence. Density dependence in the sink reduces, but does not eliminate, the predicted effect. For populations with discrete generations, we suggest that a wide range of outcomes is possible, including depressed as well as elevated average sink abundances. One potentially important implication of these effects of temporal variation is on community structure, if sink populations interact with other species. We show that temporal variation in an open community can alter competitive dominance, typically in favor of immigrant species. The particular model we examine is a classic model of exploitative competition for a single limiting resource, occurring within a habitat patch in which a competitively inferior species is maintained by immigration from an external source.

## 2. Sink population dynamics

Consider a population in a sink habitat sustained by immigration, in the absence of which the population is expected to go extinct due to deterministic forces. Such extinction could occur because a species is maladapted to the local environment, or because of exclusion due to resident competitors and predators. We assume the population has continuous, overlapping generations. We will briefly discuss an analogous discrete generation system below, which gives different results in some cases. A general model for the continuous-time population is

$$\frac{dN}{dt} = f(t)N + I(t). \quad (1)$$

Here,  $N$  is population density,  $f(t)$  the local per capita growth rate at time  $t$ , and  $I(t)$  the immigration rate at time  $t$ . In general, the growth rate  $f(t)$  can vary through time as a function of both abiotic and biotic factors (e.g., predator abundance). We have elsewhere sketched an argument (Gonzalez and Holt, 2002) that such variation can increase the average abundance of a sink population. After presenting the basic idea, we examine

in detail the magnitude of the effect for several illuminating special cases.

Model (1) is an inhomogeneous differential equation, in which temporal variation is treated as a deterministic process. Richard Levins (1979) championed the use of time-averaging to explore the influence of deterministic patterns of temporal variation on ecological systems. Over a given time  $T$  the time-average of a variable  $X(t)$  is defined to be

$$\langle X \rangle = \left( \int_0^T X(t) dt \right) / T. \quad (2)$$

If  $X(t)$  is cyclic, we take  $T$  to be the period; in an aperiodic (but bounded) environment, we let  $T$  be indefinitely large. Given a positive  $N$  bounded away from zero, and  $T$  large, then to a good approximation  $\langle dN/dt \rangle = 0$ , and  $\langle (dN/dt)/N \rangle = 0$ . For a species to be sustained in a community without immigration, when that species is rare, its time-averaged growth rate should be positive. A sink environment for a species is thus one where its long-term average growth rate is negative in the absence of immigration.

For now, we fix immigration at a constant level, so temporal variation is expressed solely in local growth rates. We also assume that there is no direct density dependence, and let  $f(t) = r(t)$  so that model (1) becomes

$$\frac{dN}{dt} = r(t)N + I. \quad (3)$$

If  $I = 0$ , model (3) implies  $N(T) = N(0) \exp(\langle r \rangle T)$ , where  $\langle r \rangle$  is the average rate of population growth. If  $\langle r \rangle < 0$ , then  $N$  asymptotically approaches 0. In a constant environment with  $I > 0$  and  $r(t) = r < 0$ , population size equilibrates at  $N^* = I/|r|$ , where  $|r|$  denotes the absolute value of  $r$ . Thus, a sink can harbor an abundant population of a species, even if that species is being excluded from that habitat by abiotic conditions or resident competitors or predators—provided the rate of exclusion from the local environment is low, and/or immigration is high (Holt, 1993; Pulliam, 1988).

Now contrast a variable environment with a similar, but constant, environment with the same average rate of population decline. Applying time-averaging to model (3), with both sides divided by  $N$ , leads to  $\langle (dN/dt)/N \rangle = 0 = \langle r \rangle + I \langle 1/N \rangle$ . This implies  $N_h \equiv (\langle 1/N \rangle)^{-1} = I/|\langle r \rangle| = N^*$ . Here,  $N^*$  is the equilibrium density expected in a constant environment with a growth rate fixed at  $\langle r \rangle$ , and  $N_h$  is the harmonic mean abundance of the sink population in the variable environment (with the same arithmetic mean growth rate). The harmonic mean population size in the variable sink thus equals the equilibrium population size  $N^*$  expected in a constant environment with the same average rate of decline. But the arithmetic mean *always* exceeds the harmonic mean (for sets of nonidentical positive numbers), so  $N^* < \langle N \rangle$ .

Thus, temporal variation in the environment leading to variability in local growth rates *inflates* the mean abundance of a sink population, compared to the abundance expected in a constant environment with the same average rate of population decline. A microcosm experiment with the protozoan *Paramecium tetraurelia* (Gonzalez and Holt, 2002) has demonstrated this predicted effect of temporal variation.

The above argument is qualitative. To quantify the magnitude of the “inflationary” effect we must make more detailed assumptions about the temporal pattern of variation. For example, assume all growth rates are negative and the rate of change in the environment is sufficiently slow so that the population to a good approximation tracks its moving equilibrium, implying  $N(t) = I/|r(t)|$ . Because the rate of population decline is in the denominator of this expression, in populations sustained by immigration there is an emergent nonlinear relationship between realized population size and local growth rates (even though the growth model (3) is linear). Hence, by Jensen’s inequality (Hardy et al., 1952) we can infer that variation in  $r$  increases the average value of  $N$ . After Taylor expanding  $I/|r(t)|$  and dropping all but the first two terms, we find that the fractional increase in mean abundance due to the inflationary effect is proportional to  $\sigma^2/\langle r \rangle^2$ . Thus, the inflationary effect should be strongest in sink habitats where the focal species is only weakly excluded (i.e., where  $\langle r \rangle$  is near zero).

This approximation breaks down if the population does not track its equilibrium (fast environmental variation), or if there are times of positive growth. There are two general, plausible scenarios for temporal variation in a sink environment. If the average growth rate is strongly negative, and the range of variation is moderate, the habitat is always a sink (i.e., the habitat is a “persistent sink”). But for the same magnitude of variation, if the average rate of decline is sufficiently near zero, there are likely to be periods with a positive growth rate (i.e., the habitat is an “intermittent sink”). The quantitative examples explored below show that these transient periods of positive growth, if sustained, have a disproportionate effect upon the long-term average abundance of a sink population.

### 2.1. Example I: a single-species model with square-wave temporal variation

In Appendix A, we give the general form for the solution of Eq. (3). This general solution includes integrals that cannot in general be given in simple, closed form. One specific form of temporal variation which does permit a closed-form solution is to assume that immigration from the source is constant ( $I(t) = I$ ), and that temporal variation in the intrinsic rate of growth follows a square wave of period  $2T$ , with regular

shifts in  $r(t)$  between two exponential growth rates,  $r_1$  and  $r_2$ , with each phase lasting  $T$  time units. Because the habitat is a sink, we assume  $r_{av} = (r_1 + r_2)/2 < 0$ . We assume  $r_1 > r_2$ .

As shown in Appendix A, the long-term average population size of a sink population experiencing square-wave variation in its intrinsic growth rate is given by

$$\langle N \rangle = \frac{I}{2r_1r_2} \left[ -r_1 - r_2 - \frac{(r_1 - r_2)^2(1 - e^{r_1T})(1 - e^{r_2T})}{r_1r_2T(1 - e^{(r_1+r_2)T})} \right]. \quad (4)$$

There are three parameters that define temporal variation in this sink environment: the growth rate during good times, the growth rate during bad times, and the length of the period. Equivalently, the environment is characterized by the average growth rate over a complete cycle ( $r_{av}$ ), the difference between good and bad years (the variability of the environment,  $r_1 - r_2 = 2\Delta r$ ), and the period of the cycle (see Fig. 1). With this pattern of environmental variation, equilibrational population dynamics in the sink shows a rhythmic

pattern of growth, followed by exponential decline (Fig. 2).

Using expression (4), in Figs. 3–5, we portray how average abundance depends upon the average growth rate and the magnitude and temporal pattern of variation in the sink. In the example shown in Fig. 3 (corresponding to the pattern of variation shown in Fig. 1b), the intrinsic growth rate is negative in both good and bad years. An increase in the period (i.e., the length of runs of good and bad years) does increase average population size over the cycle, but only to a modest extent.

By contrast, consider now the examples shown in Figs. 4 and 5 (matching the variation in an intermittent sink shown in Fig. 1a). Here, in each case, the parameters are chosen such that in a closed environment, the species goes extinct (i.e., its average growth rate is negative). But in an open environment, the species is maintained locally because of immigration, and during runs of good years it enjoys a positive growth rate. During runs of bad years, the population asymptotically approaches an abundance of  $I/|r_2|$ . This defines a “floor” of abundance, from which the population can then rebound when conditions improve. The effect of temporal variation is to increase  $\langle N \rangle$ , sometimes dramatically. The effect increases with

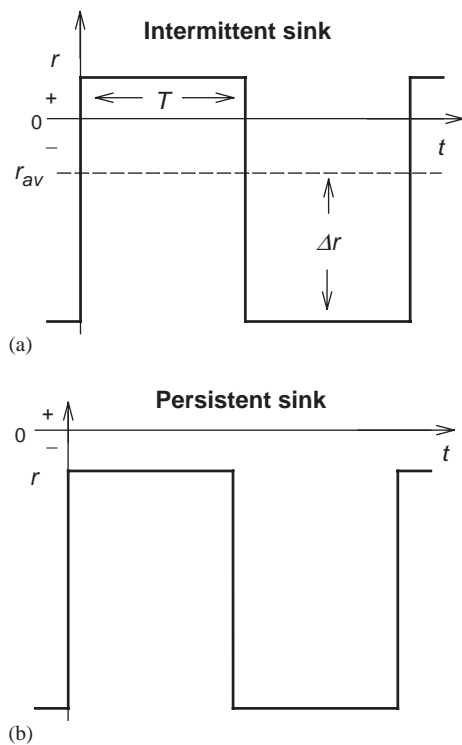


Fig. 1. Plots of square wave  $r(t)$  for an intermittent sink and a persistent sink. The square wave pattern of environmental variation is defined by average growth rate ( $r_{av}$ ), range in growth rate ( $2\Delta r$ ) and period ( $2T$ ).

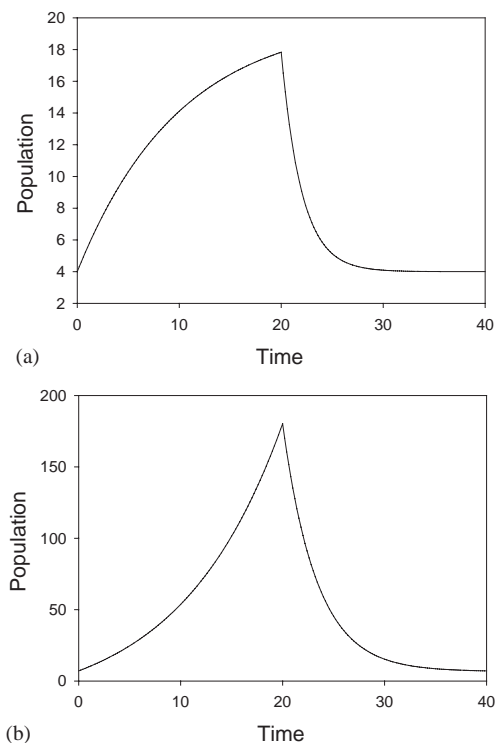


Fig. 2. Time plots of a sink population with square wave variation in growth rate and constant immigration. The growth model is  $dN/dt = r(t)N + I$ , with  $I = 2$  and  $T = 20$ . For (a),  $r_{av} = -0.3$  and  $\Delta r = 0.2$  (persistent sink) while for (b),  $r_{av} = -0.1$  and  $\Delta r = 0.2$  (intermittent sink).

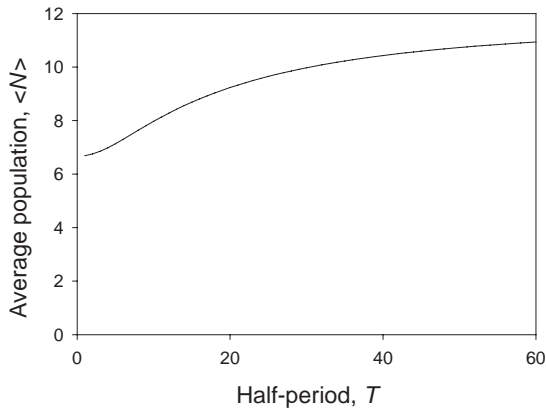


Fig. 3. Average population as a function of half-period  $T$  for persistent sink. Model and parameters as in Fig. 2a.

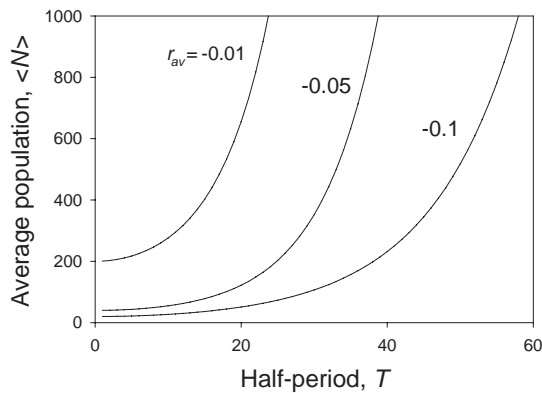


Fig. 4. Average population size as a function of half-period  $T$  for an intermittent sink, for different average growth rates (constant  $\Delta r = 0.2$  and  $I = 2$ ), same model as Fig. 2.

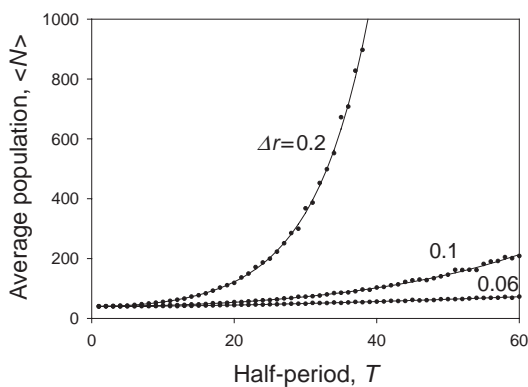


Fig. 5. Average population size as a function of half-period  $T$  for an intermittent sink, for different ranges of environmental variation  $\Delta r$  (average growth rate =  $-0.05$  and  $I = 2$ ), for the system of Fig. 2. The circles are from a numerical solution for the equivalent discrete population model with Poisson processes for births, deaths and immigrants, with birth rate and immigration rate constant and death rate a square wave. For this discrete model of demographic stochasticity, the immigration rate is 2, the birth rate is 0.2 and the death rate has an average of 0.25 and  $\Delta d$  of 0.2, 0.1 and 0.06 from left to right (see Appendix B).

increasing period, because the population can exponentially spike to higher abundances during long runs of good years. Moreover, this inflationary effect of temporal variation in the sink is larger, the milder the sink is on average (i.e., the closer the average rate of decline is to zero, see Fig. 4). The reason is that a lower rate of decline sustains a population at a higher floor, which in turn permits it to then achieve higher abundances during good years (a higher  $r_{av}$  also implies a higher growth rate in good years, for the same  $\Delta r$ ). Finally, for a given average rate of decline, the inflationary effect is larger when the amplitude of variation in growth is greater (see Fig. 5), again because the benefit of exponential growth in good years outweighs the cost of exponential decline in bad years.

The model thus illustrates three different aspects of sink environments which must be considered to understand population dynamics: (1) the “severity” of the sink environment (measured by  $\langle r \rangle = r_{av}$ ), (2) the “intermittency” of the sink condition (i.e., are there periods of positive growth?), and (3) the length of “runs” of good and bad years (in this case, measured by  $T$ ). The inflationary effect of temporal variation should be particularly marked in mild, intermittent sinks with long runs of good years.

2.2. Example II: a single-species model incorporating demographic stochasticity

Model (3) assumes that population abundance is sufficiently large to be treated as a continuous variable. This assumption may not be reasonable in a temporally varying sink environment, where it is possible for populations to reach low absolute abundances. We have carried out numerical studies of a model analogous to (3), in which discrete individuals give birth, die, and immigrate, and there is square-wave variation in per capita death rates. This model is an extension of a classic individual birth–death–immigration model (Bartlett, 1960; Renshaw, 1991). The details of our simulation protocol are described in Appendix B. The dots in Fig. 5 describe the long-term average abundance of sink populations with demographic stochasticity experiencing square-wave variation in per capita death rates. As can be seen, the analytic results for model (3) assuming a continuously varying population and square-wave variation in  $r(t)$  match quite well the outcome of these individual-based simulations. The prediction of an inflationary effect of temporal variation on sink abundance thus appears both qualitatively and quantitatively robust to demographic stochasticity, at least in this example.

2.3. Example III: stochastic variation in  $r$

Square-wave deterministic variation is of course a rather artificial pattern of temporal variation. As a step

towards generality, consider now a system in which the intrinsic growth rate is a normally distributed random process, with a defined autocorrelation structure (see Appendix C for details). Fig. 6 shows some typical population trajectories generated by this process. Basically, in an autocorrelated sink environment, one observes a pattern of population fluctuations around a low level maintained by immigration, punctuated by sporadic outbreaks to high density. By inspection of the example in Fig. 6, one can see that the effect of environmental autocorrelation is to greatly increase the magnitude of the peaks during runs of good years, compared to the numerical troughs achieved during runs of bad years (note that density is shown on a logarithmic scale).

Fig. 7 shows an example of how average population size (calculated over 10,000 time units in the simulation) is inflated by autocorrelated temporal variation in  $r$ . In such simulations, in general the long-term average population size tends to increase if: (i) the average rate of population decline is not far below zero, (ii) temporal variation in  $r$  is high, and (iii) autocorrelation in growth rates is large. Each of these increases the probability of longer runs of positive growth rate. These results match those described earlier for deterministic square-wave variation.

As shown in Appendix C, in this model the average population size achieves a finite value only if  $\bar{r} + \sigma^2 t_c < 0$ , where  $\bar{r}$  is the mean (negative) growth rate,  $\sigma^2$  is the variance in the growth rate, and  $t_c$  is the autocorrelation time constant. If this inequality is violated, population outbreaks reach such an extreme and so frequently that there is no longer a finite expected value. If this inequality is satisfied, it can be shown that  $\langle N \rangle$  increases with increasing  $\sigma^2$  and  $t_c$  (results not shown).

2.4. Example IV: a single species sink model with density dependence

Hence, if variance in  $r$  is too large in this model of a randomly varying sink population, then  $\langle N \rangle$  tends towards infinity. Basically, mean abundance is undefined, given the fat “tail” of abundances generated by the random process. Although of mathematical interest, in this limit the model surely loses biological plausibility, basically because we have assumed no feedback between local population growth rate and local population size. The assumption of no direct density dependence in local growth becomes dubious whenever populations can outbreak to high densities, which is likely in strongly autocorrelated environments.

Numerical studies show that direct density dependence weakens, but does not eliminate, the inflationary effect of temporal variation in the sink. Fig. 8 depicts how average abundance varies with the magnitude

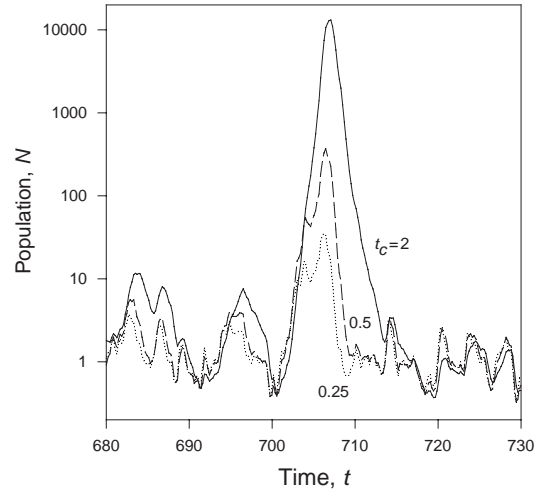


Fig. 6. Time plots for a sink population with random (Gaussian) growth rate and constant immigration, and density dependence.  $dN/dt = (r - dN)N + I$ , with  $I = 1$ ,  $d = 0.0001$ , mean  $r = -1$ , standard deviation of  $r = 1.5$ , and autocorrelation time constant of  $r$  as indicated in figure (see text for details).

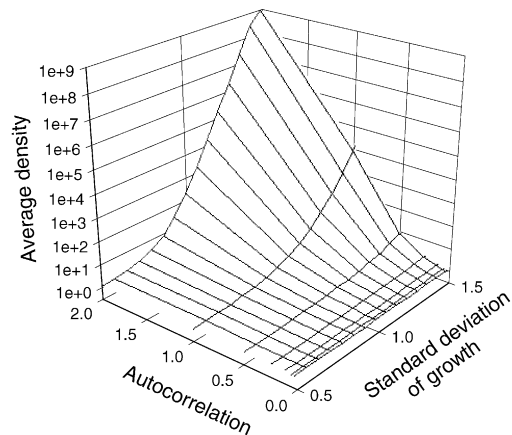


Fig. 7. Average population series as a function of autocorrelation time constant and growth rate standard deviation, for the system of Fig. 6 with  $I = 1$ , mean  $r = -1$  and  $d = 0$  (no density dependence). The population is averaged over 10,000 time units. For points such that  $\sigma^2 t_c > |\bar{r}| = 1$ , the variance of the estimated average population was very large and increased as the period over which the average was calculated was increased. As shown in Appendix C, the theoretical average for these points is infinite.

of variation and autocorrelation for a stochastic model similar to the one explored in Appendix C, except that now we assume the per capita population growth rate at time  $t$  to be  $f(t) = r(t) - dN(t)$ , where  $r(t)$  is a time-varying per capita rate of density-independent growth, and  $d$  is a measure of the strength of direct density dependence in the sink environment. If density dependence in the sink habitat is weak (Fig. 8a), the inflationary effect is strong. If density dependence instead is moderate (Fig. 8b), the inflationary effect is reduced, but can be quite large in

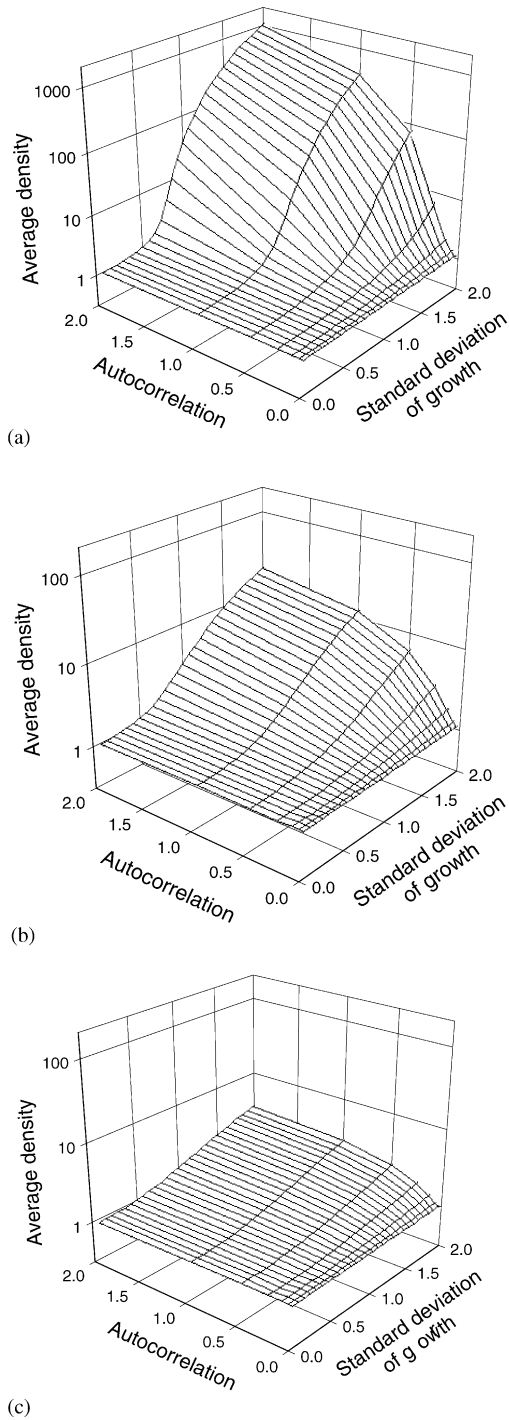


Fig. 8. Average density, comparable to Fig. 7 except including density dependence. (a)  $d = 0.0001$  (b)  $d = 0.01$  and (c)  $d = 0.1$ .

strongly autocorrelated variable environments. The stronger is density dependence in the sink, the weaker is the inflationary effect of temporal variation (Fig. 8c).

In general, there seems to be little known empirically about the nature and magnitude of density dependence in sink populations. The factor(s) causing exclusion may or may not be related to the strength of density

dependence during outbreaks. Density dependence may be strong when the sink habitat is particularly bad. Or, there may be very weak direct density dependence in the sink, as has been observed in some well-studied sink populations, e.g., Keddy (1981, 1982). In the next section, we examine a biologically plausible model system in which the mechanism leading to both sink conditions and density dependence in the sink arises explicitly from a well-known mechanism—exploitative competition for a limiting resource. The model illuminates the potential role of the “inflationary” effect of variation in sink populations as a factor constraining community structure.

### 3. Competitive interactions in a sink environment

If temporal variation increases the abundance of a given immigrant species in a sink environment, this can enhance the impact of this species upon other, resident species. Consider a system with two competing species in a landscape with two distinct habitats. Species 1 is superior at competing in habitat 1, and species 2 in habitat 2. If each habitat is closed to movement, the system should equilibrate in a state in which each species respectively dominates the habitat in which it is superior. But if movement occurs and is also strongly asymmetrical (e.g., due to spatial variation in environmental productivity or directional dispersal), a species may be excluded even from a habitat in which it is competitively superior, given sufficient inputs of an inferior competitor.

To our knowledge, the first ecologists to recognize this effect were Fenchel and Christensen (1977), who examined a Lotka–Volterra model of direct competition in a habitat patch in which one species occurred, without immigration, and a second competing species was augmented by recurrent immigration from an external source. Fenchel and Christensen (1977) showed theoretically that high rates of immigration could lead to exclusion of the non-immigrating species, and suggested that this scenario could explain some patterns in the distribution of two species of marine snails in Denmark. Recently, one of us (Holt, in press) has examined the same scenario for a model of indirect, exploitative competition for a single limiting resource. Here, we first sketch this general model for exploitative competition in a constant environment with asymmetrical inputs by an inferior competitor, and then demonstrate that temporal variation often increases the likelihood that the immigrant inferior species will supplant a locally superior, but non-immigrant, competitor.

Consider the following model for two species competing for a single limiting resource, with no direct density dependence in local growth rates (consumer density

dependence is mediated via resource consumption):

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[g_1(R) - m_1] = N_1f_1(R), \\ \frac{dN_2}{dt} &= N_2[g_2(R) - m_2] + I = N_2f_2(R) + I, \\ \frac{dR}{dt} &= G - N_1g_1(R) - N_2g_2(R).\end{aligned}\quad (5)$$

For simplicity, this model assumes that abundances are measured on scales such that each unit of resource consumed translates into an equivalent number of consumers born. The quantity  $g_i(R)$  is the birth rate of consumer  $i$  ( $i = 1, 2$ ), which is a function of  $R$ , the abundance of the limiting resource. Consumer  $i$  has a density-independent rate of mortality (including emigration) of  $m_i$ , and the net per capita growth rate of species  $i$  is  $f_i(R) = g_i(R) - m_i$ . Species 2 has an immigration rate of  $I$  (individuals per unit time), and resource renewal is given by  $G$ . In general,  $G$  varies with  $R$ . For instance,  $G = rR(1 - R/K)$  describes a biotic resource (logistic growth, with  $r$  and  $K$ , respectively, being the resource intrinsic growth rate and carrying capacity), and  $G = J - \mu R$  an abiotic resource ( $J$  measures resource renewal, and  $\mu$  gauges resource loss). We use the latter functional form for resource renewal in the example of temporal variation presented below.

As is well-known (Tilman, 1982; Grover, 1997), in a closed environment (viz.,  $I = 0$ ), if the system settles into an equilibrium, one competitor will eliminate the other, with the winner being that species which can persist at the lower level of resource. Let  $R_i^*$  denote the resource level at which consumer species  $i$  has a birth rate matching its death rate. The species with lower  $R_i^*$  wins in a closed environment, and the other competing species should be eliminated. But if the competitively inferior species (i.e., the one with higher  $R_i^*$ ) has its numbers augmented by recurrent immigration, then it will clearly persist. Moreover, if its immigration rate is sufficiently high, the superior species can be locally eliminated. The condition for this to occur is

$$I \geq G \frac{|f_2(R_1^*)|}{g_2(R_1^*)} \quad (6)$$

(see Holt, in press for more details). This expression implies that reversal of local competitive dominance may occur given (i) weak competitive exclusion (the quantity  $|f_2(R_1^*)|$  measures the rate of exclusion of species 2, when species 1 is at equilibrium with the resource), (ii) an unproductive local environment (i.e., low  $G$ ), and (iii) a high immigration rate for the inferior competitor. Basically, competitive reversal occurs when immigration permits the inferior species to be present in sufficiently high numbers to push resources to a level below the required  $R^*$  for the dominant competitor.

What is the effect of temporal variation upon this reversal of local competitive dominance? A heuristic

argument suggests that variation should enhance the impact of the immigrating species upon the resident, superior species, making it more likely the latter will be depressed in abundance, or even supplanted. In considering model (3), we saw that temporal variation tends to increase average population size for a sink population. A habitat in which a superior competitor resides, and an inferior competitor persists only because of immigration, defines a sink environment for the latter. Our analyses of model (3) suggest that temporal variation increases average abundance of a sink population. Because each individual consumes resources, the net impact of the immigrant species upon the local resource pool should thus be enhanced in variable environments. This should imply that less resource should on average be available for the resident, superior species, whose numbers should correspondingly be depressed.

This heuristic argument ignores the effects of density-dependent feedbacks between inflated abundance and average growth for the immigrant species (which we have seen reduces the expected magnitude of inflation, see Fig. 8), and also does not tell us if the effect is sufficiently strong to generate competitive reversal. To explore competitive reversal in more detail, we have numerically studied a special case of the above model, in which each parameter is respectively allowed to vary sinusoidally.

The special case of model (5) we consider is as follows:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1[a_1(t)R - m_1(t)], \\ \frac{dN_2}{dt} &= N_2[a_2(t)R - m_2(t)] + I(t), \\ \frac{dR}{dt} &= J(t) - \mu(t)R - [a_1(t)N_1 + a_2(t)N_2]R.\end{aligned}\quad (7)$$

Here,  $a_i$  is the attack rate by consumer  $i$  upon the resource, and the other parameters are as defined above. The two consumers have linear functional and numerical responses to the shared resource, and the resource is assumed to be abiotic.

The several panels of Fig. 9 show examples of how time-averaged consumer abundances vary as a function of the magnitude of variation in each model parameter. The parameters are chosen such that in the absence of variation (but with immigration by the inferior species), there is equal abundance for the two competing species.

Before considering these results, it is useful to understand the consequences of temporal variation in the absence of immigration. Without immigration, temporal variation in most parameters in the model does not permit coexistence or reverse competitive dominance. The one exception is variation in  $a_1$ . If variation in the attack rate of the superior competitor is sufficiently large, the inferior species can persist.



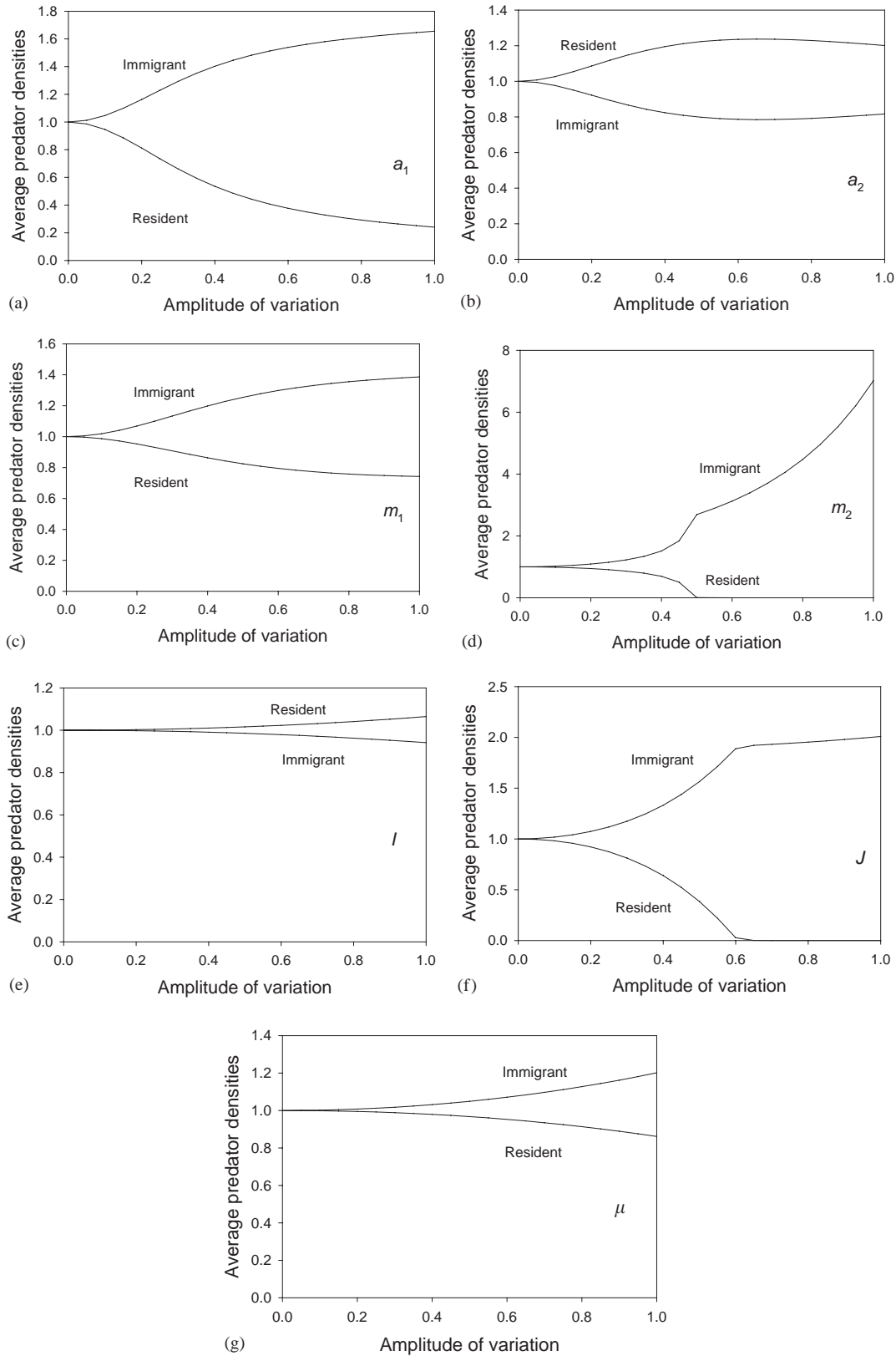


Fig. 9. Average population of the two consumers in system with a resource and two consumers (the inferior of which has immigration), with one parameter varying sinusoidally.  $dN_1/dt = (a_1R - m_1)N_1$ ,  $dN_2/dt = (a_2R - m_2)N_2 + I$ ,  $dR/dt = J - R(a_1N_1 + a_2N_2 + \mu)$ .  $a_1 = a_2 = 0.1$ ,  $m_1 = 1$ ,  $m_2 = 1.1$ ,  $I = 0.1$ ,  $J = 3$  and  $\mu = 0.1$ . When a given parameter varies, it has the form  $y(t) = y_{av}[1 + x \sin(2\pi ft)]$ , where the frequency  $f = 0.05$ ,  $x$  is the value on the abscissa of the graph, and  $y_{av}$  is equal to the value given above (which is also the constant value of the parameters that are not varying). The time-varying parameters are respectively: (a)  $a_1$  (b)  $a_2$  (c)  $m_1$  (d)  $m_2$  (e)  $I$  (f)  $J$  (g)  $\mu$ .

To see why this occurs, consider the following argument. Assume that species 2 in model (7) is competitively inferior in a constant environment, which means it has a higher resource requirement, and that  $I = 0$ . We will use an asterisk (\*) to indicate a parameter value in a constant environment; for instance,  $m_i^*$  will denote the death rate of species  $i$  in a constant environment. In such an environment, species  $i$  has a required resource level of  $R_i^* = m_i^*/a_i^*$ . The species with lower  $R_i^*$  wins (Tilman, 1982; Grover, 1997). Assume for now that the attack rates are constant, but one or more of the other parameters are time-varying. If species 1 is present, then we can time-average its per-capita growth rate, leading to a time-averaged resource abundance of  $\langle R \rangle_1 = \frac{\langle m_1 \rangle}{a_1^*}$ . If species 2 now attempts to invade, its average per capita growth rate is  $a_2^* \langle R \rangle_1 - \langle m_2 \rangle$ , which is positive only if  $\langle R \rangle_1 > \frac{\langle m_2 \rangle}{a_2^*}$ , or  $\frac{\langle m_1 \rangle}{a_1^*} > \frac{\langle m_2 \rangle}{a_2^*}$ . But this in turn implies that species 2 is a superior competitor for the resource, since were it present alone it would push average resource to  $\langle m_2 \rangle/a_2^*$ , which is a level insufficient for species 1. Hence, if the variable environment has the same average mortality rate as does the constant environment, we see that variation in mortality rates or resource renewal and loss rates ( $J$  and  $\mu$ ) does not by itself alter the outcome of exploitation competition.

By contrast, temporal variation that affects the attack rates of species 1 can facilitate invasion by species 2. Assume that species 1 is alone, and that  $a_1$  varies slowly, so that to a reasonable approximation,  $R(t) \approx \frac{m_1}{a_1(t)}$ . Now let species 2 attempt to invade. Its long-term average growth rate is  $\langle a_2(t)R(t) - m_2 \rangle \approx \langle \frac{a_2(t)}{a_1(t)} \rangle m_1^* - m_2^*$ . If species 2 has a constant attack rate, but species 1 a variable attack rate, by Jensen's inequality we see that species 2 enjoys elevated resource levels and so is more likely to invade. Conversely, given our assumptions, species 1 can invade when species 2 is present and at equilibrium.

If instead the inferior competitor alone experiences variable attack rates, this does not permit coexistence or competitive reversal. In this case, if species 1 is present, the resource equilibrates at a constant level of  $R_1^* = \frac{m_1^*}{a_1^*}$ . The time-varying per capita growth rate of species 2, when rare, is  $\langle a_2(t)R_1^* - m_2 \rangle = \langle a_2 \rangle R_1^* - m_2^*$ . But this is negative, because  $\langle a_2 \rangle = a_2^*$ , and by assumption  $R_2^* > R_1^*$ . Finally, if the attack rates vary slowly and synchronously, so that we can write  $a_i(t) \equiv a_i' \phi(t)$ , where  $a_i'$  is a constant and  $\phi(t)$  is a time-varying function shared by the two species, this variation disappears from the expression for long-term growth rate; in this model, shared temporal variation has no impact upon the average rate of invasion of species 2, or on the reciprocal ability of species 1 to invade when it is rare.

In short, without immigration, temporal variation in most parameters of this model does not prevent

competitive exclusion, and it does not lead at all to competitive reversals. (As an aside, we are unaware of prior demonstration that variability in attack rates alone can permit coexistence of exploitative competitors, if such variability is differentially experienced by the superior competitor. The effect arises even with the simplest, linear functional response.)

By contrast, given immigration, temporal variation in *all* of the parameters in the model influences the competitive interaction, either shifting relative average abundance or even reversing competitive dominance. There are moreover qualitative differences in the impact of temporal variation, depending upon which model parameter is time-varying. In the example shown in the various panels of Fig. 9, temporal variation can at times increase the advantage of the locally superior species, depressing the abundance of the immigrating inferior competitor. This characterizes variation expressed via the consumption rate of the inferior competitor on the resource ( $a_2$ ) and the immigration rate of the inferior competitor ( $I$ ). But in other cases, temporal variation reduces the abundance of the locally superior species. This describes variation in the mortality rate of both competitors (the  $m_i$ ), variation in the attack rate of the superior competitor ( $a_1$ ), and variation in basal productivity (either  $J$  or  $\mu$ ).

Moreover, variation in the death rate of the inferior competitor, or in basal productivity, can lead to the exclusion of a superior competitor that would be expected to persist in a constant environment. Synchronous variation in species attack rates or death rates also can shift competitive dominance (Fig. 10). None of these effects arise in a system that is temporally varying but closed to immigration.

This example illustrates that temporal variation in open communities can have a variety of effects upon competitive coexistence, depending upon which facet of the system varies, and the magnitude of such variation. The results described in the figure characterize impacts of temporal variation upon average abundance. Another effect of temporal variation is to increase the frequency of excursions to low densities, which makes it more likely that a species not able to immigrate from an external source pool will suffer extinction due to demographic stochasticity. Fig. 11a shows an example of trajectories generated with sinusoidal variation in mortality of the inferior competitor, and Fig. 11b describes how the average and minimal abundances of the superior competitor shift with increased variation in the mortality of the inferior competitor. Given that local extinctions are likely to occur due to demographic stochasticity when populations drop to very low levels, even modest amounts of variation in mortality for the immigrant, inferior species can tilt the competitive interaction in its favor, permitting it to supplant a locally superior but non-immigrating species.

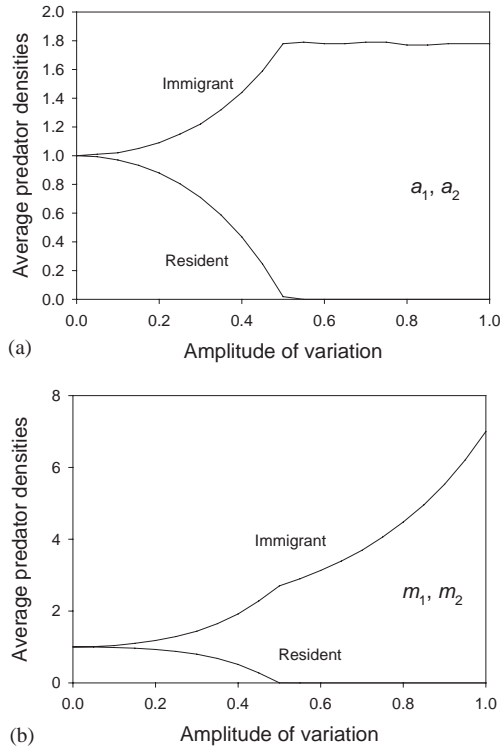


Fig. 10. Average population, comparable to Fig. 9, but with two parameters varying in phase: (a)  $a_1$  and  $a_2$  (b)  $m_1$  and  $m_2$ .

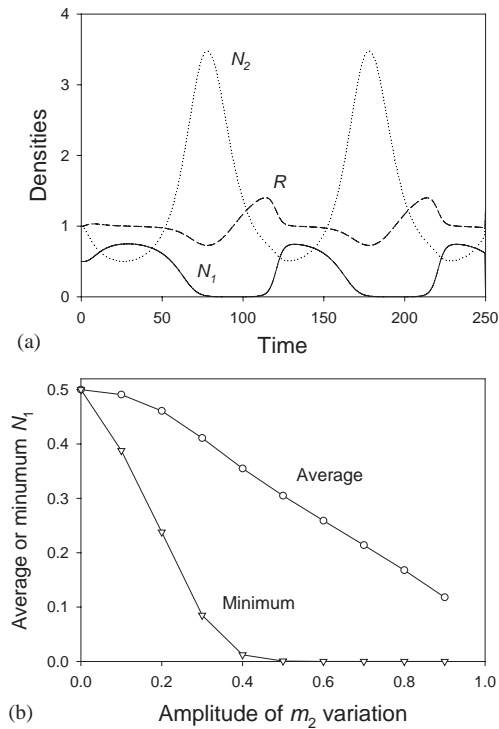


Fig. 11. Population trajectory for the model of Fig. 9, with  $a_1 = 1$ ,  $a_2 = 0.5$ ,  $m_1 = 1$ ,  $m_2(\text{average}) = 1$ ,  $I = 0.5$ ,  $J = 2$  and  $\mu = 1$  and  $f = 0.01$ . (a) Time plots of the three species for an amplitude of  $m_2$  variation of 0.5. (b) Average and minimum values of the superior competitor as a function of amplitude of variation of the death rate of the inferior competitor.

#### 4. Conclusions

There is growing evidence from a diverse range of ecological systems that local population, community, and ecosystem dynamics are profoundly altered by flows of organisms and materials in space (Holt, 1993; Polis et al., 1997; in press). Because of asymmetries in local productivity or dispersal, such flows can lead to sink populations, where species are maintained by immigration in habitats from which they tend to be excluded (e.g., due to intolerance of abiotic conditions, or competing species). Most environments are also variable on various time-scales, due both to extrinsic forcing and endogenous sources of instability. In this paper, we have argued that temporal variation often enhances the time-averaged abundance of sink populations—a phenomenon we have dubbed the “inflationary” effect of variation. Using time-averaging, a simple argument shows that inflation is a generic feature of temporal variation in sink habitats described by continuous-time models without density dependence. To illustrate the effect and explore it in greater detail, we have examined several more specific models, both analytically and numerically. These studies show that the inflationary effect is particularly strong if sinks are (i) weak, so that the average rate of decline is not far below zero, (ii) intermittent, with some periods of positive growth, and (iii) autocorrelated, leading to runs of good years.

This effect may be particularly relevant when one considers that set of species in a regional species pool which on average are excluded from local communities by interspecific interactions such as competition and predation. The strength of interspecific interactions by residents upon an invading species typically scales with the population sizes of resident species. Population abundances are typically both variable and autocorrelated, and so the rate of exclusion should itself be variable and autocorrelated. In general, species which are weakly excluded from a local community may nonetheless on average be common there, if they enjoy recurrent immigration from an external source pool and transient phases of positive growth due to environmental fluctuations (with concomitant variation in the abundances of resident community members).

Such species in turn can exert strong effects upon the resident community. In this paper, we illustrated this possibility with a model in which a species that is inferior at competing for a shared resource is maintained by immigration in a habitat patch containing a resident, superior competitor. Generally (though not always), temporal variation increases the abundance of the inferior competitor, and decreases the abundance of the superior competitor. The effect can be so pronounced that the superior species is even driven to extinction in the variable environment. In effect, temporal variation magnifies the impact of regional

processes, mediated via immigration, as determinants of local community structure in guilds of competing species.

With a one-population, discrete-generation model analogous to model (3), positively autocorrelated temporal variation in the growth rate generally leads to inflation of the average abundance of  $N$ , as it did for the continuous-time model. However, if the growth rate is an uncorrelated random process, its variation has no effect on the average population size. If successive values of the growth rate are negatively correlated, the average value of  $N$  can be depressed. To see these effects, consider the discrete generation model  $N(t+1) = N(t)R(t) + I(t)$ . Taking expectations on both sides and solving for the expected population size, we have  $E(N) = [E(I) + \text{cov}(N, R)]/[1 - E(R)]$ , where  $E$  denotes expected value, and  $\text{cov}(N, R)$  is the covariance of  $N$  and  $R$ . If  $N$  and  $R$  are statistically uncorrelated, then the expected value of  $N$  is unchanged by temporal variation in the sink. The sign of the covariance term can in general be either positive or negative. Even in the absence of density dependence, autocorrelation in  $R$  will lead to a non-zero covariance term. A two-point cycle in  $R$ , for instance, leads to a negative covariance between  $N$  and  $R$ , and so lowers average population size. Density dependence (which can be represented by expressing  $R$  as a function jointly of density and a time-varying environmental factor) can also influence the sign and magnitude of the covariance term. For instance, if there is positive density dependence in the sink habitat (e.g., an Allee effect at low densities), then even uncorrelated temporal variation in environmental factors influencing  $R$  can lead to a positive covariance term. We plan to discuss discrete-time systems in more detail in a future publication.

Over evolutionary time-scales, temporal variation is believed to be a primary driver of the evolution of elevated dispersal rates, compared to constant environments. This in turn increases the magnitude of spatial fluxes, creating the potential for strong, asymmetrical fluxes between habitats varying in population size and productivity. An important challenge for ecologists is to assess the interplay of temporal variation and spatial heterogeneity in determining species' abundances and constraints on species coexistence in local communities. We suggest that our results highlight some of the surprising things that can happen when one overlays temporal variation upon spatially heterogeneous landscapes.

## Acknowledgments

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## Appendix A. A sink population with square-wave variation in growth rates

The system consisting of one species with time-varying growth rate and immigration can be described by the following inhomogeneous differential equation:

$$\frac{dN}{dt} = r(t)N(t) + I(t). \quad (\text{A.1})$$

The solution to (A.1) is

$$N(t) = e^{\int_{t_0}^t r(\tau) d\tau} \left[ N(t_0) + \int_{t_0}^t I(u) e^{-\int_{t_0}^u r(\tau) d\tau} du \right]. \quad (\text{A.2})$$

We will assume that  $I$  is constant and  $r(t)$  is a square wave and thus is constant over intervals (half the period) of length  $T$ . Over one of these intervals, (A.2) can be solved assuming constant  $I$  and  $r$ , giving:

$$N(t) = e^{r(t-t_0)} \left[ N(t_0) + \frac{I}{r} \right] - \frac{I}{r}. \quad (\text{A.3})$$

Let the first interval start at  $t = 0$  and have growth rate  $r_1$ . Then, using (A.3):

$$N(T) = e^{r_1 T} \left[ N(0) + \frac{I}{r_1} \right] - \frac{I}{r_1}. \quad (\text{A.4})$$

The second interval starts at  $t = T$  and has growth rate  $r_2$ , so we can use (A.3) and (A.4) to solve for  $N(2T)$  in terms of  $N(0)$ .

$$\begin{aligned} N(2T) &= e^{r_2 T} \left[ N(T) + \frac{I}{r_2} \right] - \frac{I}{r_2} \\ &= e^{r_2 T} \left[ e^{r_1 T} \left\{ N(0) + \frac{I}{r_1} \right\} - \frac{I}{r_1} + \frac{I}{r_2} \right] - \frac{I}{r_2} \\ &= N(0). \end{aligned} \quad (\text{A.5})$$

If  $N(t)$  is periodic (with the same period as  $r$ ), then  $N(2T)$  must equal  $N(0)$ , which allows us to solve for  $N(0)$ :

$$N(0) = I \left[ \frac{e^{(r_1+r_2)T}}{r_1} + \left( \frac{1}{r_2} - \frac{1}{r_1} \right) e^{r_2 T} - \frac{1}{r_2} \right] / [1 - e^{(r_1+r_2)T}]. \quad (\text{A.6})$$

We can also solve for  $N(T)$  using (A.4) and (A.6):

$$N(T) = I \left[ \frac{e^{(r_1+r_2)T}}{r_2} + \left( \frac{1}{r_1} - \frac{1}{r_2} \right) e^{r_1 T} - \frac{1}{r_1} \right] / [1 - e^{(r_1+r_2)T}]. \quad (\text{A.7})$$

With these values and (A.3) above, we have an expression for  $N(t)$  over an entire period, from which

we can calculate the average value:

$$\begin{aligned} \langle N \rangle &= \frac{1}{2T} \int_0^{2T} N(t) dt \\ &= \frac{1}{2T} \left[ \int_0^T e^{r_1 t} \left\{ N(0) + \frac{I}{r_1} \right\} \right. \\ &\quad \left. - \frac{I}{r_1} dt + \int_T^{2T} e^{r_2(t-T)} \left\{ N(T) + \frac{I}{r_2} \right\} - \frac{I}{r_2} dt \right], \end{aligned}$$

leading to the expression given in the text,

$$\langle N \rangle = \frac{I}{2r_1 r_2} \left[ -r_1 - r_2 - \frac{(r_1 - r_2)^2 (1 - e^{r_1 T})(1 - e^{r_2 T})}{r_1 r_2 T (1 - e^{(r_1 + r_2) T})} \right]. \quad (\text{A.8})$$

**Appendix B. A sink population with demographic stochasticity**

A classic birth–death–immigration process model of demographic stochasticity in a constant sink environment without density dependence was studied by Bartlett (1960, see Renshaw, 1991, pp. 41–44). Assume that in a short time-interval  $(t, t+h)$ ,  $bh$  is the probability of a birth to an individual in a population of size  $N$ ,  $dh$  is the probability of an individual’s death, and  $Ih$  is the probability an immigrant arrives. In a constant environment, these parameters are constants; in a sink,  $d > b$ . Given these assumptions, equilibril mean population size is  $N^* = I/(d - b)$ . Note this closely matches the expression for equilibril abundance for the deterministic model (3),  $N^* = I/|r|$ .

We explored the implications of demographic stochasticity for inflation in a sink by introducing temporal variation in individual death probabilities. A Fortran program was written to simulate a population with a square-wave death rate, constant birth rate and immigration rate, and to calculate the average population. Events were assumed to be Poisson processes. In the program, individual events (births, deaths, immigrants) were simulated, and the time index and total population adjusted at each event. The total event rate was  $E = I + (b + d)N$ , where  $I$  is the immigration rate,  $b$  is the birth rate and  $d$  is the death rate, and  $N$  is the population size. Since these are Poisson processes, we can add the rates together, and the time to the next event is exponentially distributed with mean  $1/E$ . This is simulated using  $-\ln(\text{ran})/E$ , where  $\text{ran}$  is a uniform random deviate. After the time to the next event is calculated, it is assigned to immigration, death or birth by using another uniform random deviate and the relative probabilities of the three events ( $I/E$ ,  $bN/E$  and  $dN/E$ , respectively). So if this random deviate is

$< I/E$ , the event is an immigration; if it is between  $I/E$  and  $I/E + bN/E$ , it is a birth; otherwise, it is a death.

A potential problem occurs if the calculated time to the next event exceeds the time remaining in the current half-period. Since the death rate will have changed, this value cannot be used, so it is thrown out and the time advanced to the start of the next half-cycle, and then another time to the next event calculated (using the new death rate, of course). This should yield the correct results, since Poisson processes are memoryless—the distribution of the time to the next event is independent of the time since the last event. So given that an event does not occur during the rest of the current half-cycle, the time from the start of the next half-cycle to the next event is exponentially distributed with mean  $1/E$ . Numerous simulations were run to ensure that all events occurred at the proper rate during each half-cycle with this method.

Two parameters were varied—the difference in the two death rates ( $\Delta d$ ) and the period ( $2T$ ). The birth rate  $b$  was 1.3 for the set of simulations used to generate the results compiled in Fig. 12. The mean value of the death rate was 1.5 and  $\Delta d$  was varied from 0 to 0.5 in increments of 0.1 (so for  $\Delta d = 0, 0.1$  and  $0.2$ , the birth rate never exceeds the death rate, while for  $\Delta d > 0.2$ , it does half the time). For each value of  $\Delta d$ , the half-period was varied from 0.0625 to 16 (by successive doubling). The immigration rate  $I$  was set at 0.1, 1 and 10 for three different sets of simulations, which gave very similar results (differing only in the scale for  $\langle N \rangle$ ). Another set of simulations was run with  $I = 2$ , average  $d = 0.25$ ,  $b = 0.2$  and  $\Delta d$  to 0.06, 0.1 and 0.2, to compare with the analytic results derived for the continuous differential equation model with square-wave variation in  $r(t)$ . As shown in Fig. 5, except for some very minor randomness in the discrete simulations, the results agree quite closely. The inflationary effect of variation in a sink

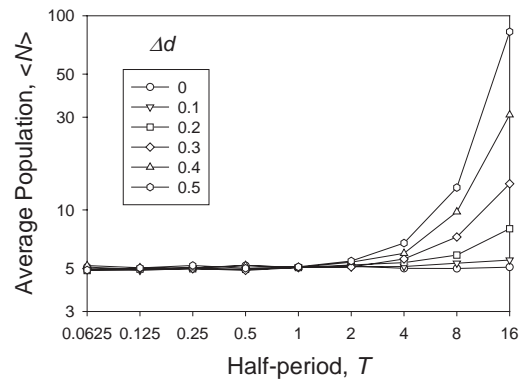


Fig. 12. Sink population dynamics with demographic stochasticity. Average population is computed for the discrete single population model with Poisson birth, death and immigration. The birth rate is 1.3 and immigration rate is 1, while the death rate is a square wave which alternates between the values  $1.5 \pm \Delta d$  every  $T$  time units, with  $T$  and  $\Delta d$  given in the figure.

appears robust to the incorporation of demographic stochasticity.

**Appendix C. A sink population with stochastic variation in growth rates**

We consider again a system consisting of a single species with time-varying growth rate and immigration described by Eq. (A.1). We assume that  $I$  is constant and  $r(t)$  is an Ornstein–Uhlenbeck process—a normally distributed random process with mean  $\bar{r}$ , variance  $\sigma^2$  and normalized autocorrelation function

$$R(\tau) = e^{-|\tau|/t_c}, \tag{C.1}$$

where  $R(\tau)$  is the correlation coefficient between values of  $r$  separated by time  $\tau$ , and  $t_c$  is the time required for this correlation to decrease by a factor of  $e$ .

We will also assume that  $N$  is initially 0, so that using Eq. (A.2)

$$N(t) = I \int_0^t e^{\int_u^t r(\tau) d\tau} du. \tag{C.2}$$

Therefore,

$$\begin{aligned} E\{N(t)\} &= E\left\{ I \int_0^t e^{\int_u^t r(\tau) d\tau} du \right\} \\ &= I \int_0^t E\left\{ e^{\int_u^t r(\tau) d\tau} \right\} du. \end{aligned} \tag{C.3}$$

Since  $r(t)$  is a normal random process, its integral is a normal random variable. If  $x$  is normal, then  $e^x$  is lognormal, and has a mean of  $e^{\mu_x + \sigma_x^2/2}$ . Letting  $x = \int_u^t r(\tau) d\tau$ ,

$$\begin{aligned} \mu_x &= E\left\{ \int_u^t r(\tau) d\tau \right\} = \int_u^t E\{r(\tau)\} d\tau \\ &= \int_u^t \bar{r} d\tau = \bar{r}(t - u), \end{aligned} \tag{C.4}$$

$$\begin{aligned} \sigma_x^2 &= E\left\{ \left( \int_u^t r(\tau) d\tau - \mu_x \right)^2 \right\} \\ &= E\left\{ \left( \int_u^t [r(\tau) - \bar{r}] d\tau \right)^2 \right\} \\ &= E\left\{ \int_u^t [r(\tau_1) - \bar{r}] d\tau_1 \int_u^t [r(\tau_2) - \bar{r}] d\tau_2 \right\} \\ &= E\left\{ \int_u^t \int_u^t [r(\tau_1) - \bar{r}][r(\tau_2) - \bar{r}] d\tau_2 d\tau_1 \right\} \\ &= \int_u^t \int_u^t E\{[r(\tau_1) - \bar{r}][r(\tau_2) - \bar{r}]\} d\tau_2 d\tau_1 \\ &= \sigma^2 \int_u^t \int_u^t \frac{E\{[r(\tau_1) - \bar{r}][r(\tau_2) - \bar{r}]\}}{\sigma^2} d\tau_2 d\tau_1. \end{aligned} \tag{C.5}$$

The integrand in the last expression is the autocorrelation function  $e^{-|\tau_1 - \tau_2|/t_c}$  (see (C.1)). Because of the

symmetry of this expression and the area of integration, the integral can be done over the region in which  $\tau_1 > \tau_2$  and the result doubled. Therefore,

$$\begin{aligned} \sigma_x^2 &= 2\sigma^2 \int_u^t e^{-\tau_1/t_c} \int_u^{\tau_1} e^{\tau_2/t_c} d\tau_2 d\tau_1 \\ &= 2\sigma^2 \int_u^t e^{-\tau_1/t_c} (t_c [e^{\tau_1/t_c} - e^{u/t_c}]) d\tau_1 \\ &= 2\sigma^2 t_c \int_u^t [1 - e^{(u-\tau_1)/t_c}] d\tau_1 \\ &= 2\sigma^2 t_c [t - u - t_c(1 - e^{-(t-u)/t_c})]. \end{aligned} \tag{C.6}$$

Hence,

$$\begin{aligned} E\{N(t)\} &= I \int_0^t \exp\{\bar{r}(t - u) + \sigma^2 t_c \\ &\quad \times [t - u - t_c(1 - e^{-(t-u)/t_c})]\} du \\ &= I e^{-\sigma^2 t_c^2} \int_0^t \exp\{(\bar{r} + \sigma^2 t_c)(t - u) \\ &\quad + \sigma^2 t_c^2 e^{-(t-u)/t_c}\} du. \end{aligned} \tag{C.7}$$

The expected value of  $N$  is an increasing function of the  $e^{-(t-u)/t_c}$  term. Since this term is always between 0 and 1, setting it equal to these values gives bounds on  $E\{N(t)\}$ :

$$\begin{aligned} I e^{-\sigma^2 t_c^2} \int_0^t e^{(\bar{r} + \sigma^2 t_c)(t-u)} du \\ < E\{N(t)\} < I e^{-\sigma^2 t_c^2} \int_0^t e^{(\bar{r} + \sigma^2 t_c)(t-u) + \sigma^2 t_c^2} du. \end{aligned} \tag{C.8}$$

Therefore,

$$\begin{aligned} - I e^{-\sigma^2 t_c^2} [1 - e^{(\bar{r} + \sigma^2 t_c)t}] / (\bar{r} + \sigma^2 t_c) \\ < E\{N(t)\} < - I [1 - e^{(\bar{r} + \sigma^2 t_c)t}] / (\bar{r} + \sigma^2 t_c). \end{aligned} \tag{C.9}$$

The average value of  $N$  from 0 to  $T$  is  $\langle N \rangle = \int_0^T N(t) dt / T$ . The expected value of this average is the average of the expected values. The bounds above (C.9) will give bounds on the average abundance.

$$\begin{aligned} - I e^{-\sigma^2 t_c^2} / [(\bar{r} + \sigma^2 t_c)T] \int_0^T 1 - e^{(\bar{r} + \sigma^2 t_c)t} dt \\ < E\{\langle N \rangle\} < - I / [(\bar{r} + \sigma^2 t_c)T] \\ &\quad \times \int_0^T 1 - e^{(\bar{r} + \sigma^2 t_c)t} dt \end{aligned} \tag{C.10}$$

or

$$\begin{aligned} - I e^{-\sigma^2 t_c^2} \left[ 1 - \frac{1 - e^{(\bar{r} + \sigma^2 t_c)T}}{-(\bar{r} + \sigma^2 t_c)T} \right] / (\bar{r} + \sigma^2 t_c) < E\{\langle N \rangle\} \\ < - I \left[ 1 - \frac{1 - e^{(\bar{r} + \sigma^2 t_c)T}}{-(\bar{r} + \sigma^2 t_c)T} \right] / (\bar{r} + \sigma^2 t_c). \end{aligned} \tag{C.11}$$

We can now take the limit as  $T$  goes to infinity to get the long-term average. This limit will only exist if  $\bar{r} + \sigma^2 t_c < 0$ , in which case

$$- I e^{-\sigma^2 t_c^2} / (\bar{r} + \sigma^2 t_c) < E\{\langle N \rangle\} < - I / (\bar{r} + \sigma^2 t_c). \tag{C.12}$$

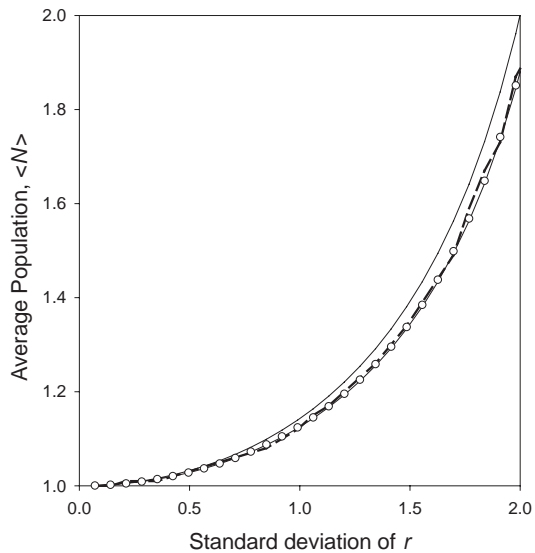


Fig. 13. Comparison of theoretical and realized bounds on average population size, given environmental stochasticity. The figure uses the system of Fig. 7. It shows a plot of the average density as a function of standard deviation of growth rate, for an autocorrelation time constant of 0.125 (dashed line) along with the upper and lower bounds as derived in the text (solid lines), and the numerical solution of the equation for  $E\{N(t)\}$  as  $t$  approaches infinity (circles).

Numerical studies show that these bounds accurately describe the long-term behavior of the system, which is also described by numerically solving (C.7) for  $E\{N(t)\}$  as  $t$  goes to infinity (see Fig. 13).

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