

THE INFLATIONARY EFFECTS OF ENVIRONMENTAL FLUCTUATIONS ENSURE THE PERSISTENCE OF SINK METAPOPULATIONS

DAVID P. MATTHEWS AND ANDREW GONZALEZ¹

Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec H3A 1B1 Canada

Abstract. Under current rates of environmental change many populations may be found in habitats of low quality and low conservation value, creating population sinks. We test recent theory that suggests, surprisingly, that stochastic environmental variability may enhance the long-term persistence of sink metapopulations. Using experimental populations of *Paramecium aurelia* we show that it is possible for a metapopulation comprised entirely of sink populations to persist for many generations in a random environment. In accordance with the theory, we show that positive temporal autocorrelation and low spatial correlation in the environment can ensure the long-term persistence and enhance the mean and maximum abundance of sink metapopulations. High levels of spatial correlation in the environment created strong population synchrony and limited the persistence time of the sink metapopulations. These results have important implications for the development of a theory underlying the synergistic effects of habitat fragmentation and environmental change on population persistence.

Key words: autocorrelation; dispersal; extinction; metapopulation; microcosm; synchrony.

INTRODUCTION

How dispersal and environmental stochasticity interact to affect the dynamics and persistence of fragmented populations is a problem of considerable pure and applied value in ecology (Earn et al. 2000, Hanski and Gaggiotti 2004). Previous theoretical studies have explored the interplay of temporal and spatial dynamics as drivers of local population dynamics (Chesson 1981, Gonzalez and Holt 2002, Haccou and Vatutin 2003, Holt et al. 2003, Roy et al. 2005) and increasing evidence shows that the movement of individuals among habitats is essential for the long-term demographic and functional integrity of populations and communities (Gonzalez et al. 1998, Hanski 1999, Loreau et al. 2003). A consequence of dispersal in heterogeneous landscapes is that individuals may move into habitats of low quality, creating population sinks. Sink populations require recurrent immigration to offset the net loss of individuals due to high rates of mortality (DeAngelis et al. 1979, Holt 1985, Pulliam 1988, 2000). By definition, the long-term intrinsic growth rate of a population sink is negative. However, there is growing empirical evidence that temporal variation in habitat quality may cause transient periods of positive growth that may lead to long-term persistence of sink populations (Virgl and Messier 2000, Johnson 2004). Here we extend recent experimental work on source–sink systems in stochastic environments (Gonzalez and Holt 2002) to

sink metapopulations in stochastic environments (Roy et al. 2005).

Gonzalez and Holt (2002) demonstrated both theoretically and experimentally that stochastic variation in growth rates can increase the mean abundance of sink populations and generate outbreak dynamics characterized by brief periods of very high abundance, also known as intermittent rarity (Ferrière and Cazelles 1999). This “inflationary effect” of the environmental variation results because sustained immigration allows rapid exploitation of intermittent periods of favorable environmental conditions that increase sink population abundance and ensure long-term persistence. The effect is strongest in autocorrelated environments, even in the presence of negative density dependence, because the periods of favorable conditions for growth tend to be aggregated in time, resulting in positive growth–density covariance (Gonzalez and Holt 2002).

This result is likely to be of broad empirical relevance because the temporal fluctuations of physical variables, such as temperature and rainfall, and the dynamics of natural populations are autocorrelated (Pimm and Redfearn 1988, Arino and Pimm 1995, Halley and Iwasa 1998, Inchausti and Halley 2001, Pelletier 2002) and because anthropogenic climate change is increasing the autocorrelation in these variables (Wigley et al. 1998). The result is also of interest because it reverses the much-studied prediction of enhanced extinction risk with increasing environmental autocorrelation in closed populations (Turelli 1977, Tuljapurkar 1982, Rotenberg 1987, Foley 1994, Johnst and Wissel 1997, Petchey et al. 1997, Pike et al. 2004, Tuljapurkar and Haridas 2006).

To date the inflationary effect has been demonstrated experimentally for the simple case of a stochastic sink

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¹ Corresponding author.

E-mail: andrew.gonzalez@mcgill.ca

coupled to a single source population (Gonzalez and Holt 2002). Recently, however, Roy et al. (2005) extended this work to consider the stochastic dynamics of a metapopulation comprised entirely of sink habitat patches (see also Jansen and Yoshimura 1998). They showed that temporal variation and moderate dispersal jointly permit the indefinite persistence of a sink metapopulation (e.g., where all subpopulations have a negative long-term geometric growth rate), provided that population fluctuations are partially spatially asynchronous. In addition, they demonstrated an inflationary effect in which positive autocorrelation both lowers the magnitude of environmental variation required for persistence and increases the average population and metapopulation abundance. However, a strengthening of spatial correlation (synchrony) across populations, due to greater rates of dispersal or large-scale climate variation (Fontaine and Gonzalez 2005), may weaken the strength of the inflationary effect on sink metapopulation persistence (Roy et al. 2005). Roy et al. (2005) did not provide experimental confirmation of their extension of the inflationary effect to sink metapopulations.

Here we present experimental results that confirm the theoretical predictions of Roy et al. (2005). Using laboratory microcosms of *Paramecium aurelia*, we have demonstrated that stochastic variation of environmental conditions coupled with moderate dispersal can permit the long-term persistence (>50 generations) of a metapopulation composed of two sink populations. Autocorrelated temperature fluctuations created positive growth–density covariance that inflated the mean and maximum metapopulation abundance. As predicted by the theory we also show that the inflationary effect on sink metapopulation abundance and persistence is strongest when there is low spatial correlation in the environmental fluctuations. These results highlight the often unintuitive nature of stochastic population dynamics, and they have broad implications for our understanding of the underlying mechanisms of species persistence and invasion in human transformed and changing environments (Schiegg 2003).

MATERIALS AND METHODS

Protist microcosms

Populations of *P. aurelia* were maintained using standard protozoan culture methods (Lawler and Morin 1993, Gonzalez and Holt 2002). A nutrient medium, made from sterile Millipore water to which 0.5 g of Carolina protozoan pellet was added per liter, was prepared in 2-L glass flasks covered with aluminum foil lids. Once autoclaved, the medium was inoculated with three bacterial species (*Serratia marcescens*, *Bacillus subtilis*, and *Bacillus cereus*) and incubated at room temperature for 48 h. Following incubation, 48 mL of inoculated medium was pipetted into each of 60 sterilized 100-mL glass screw-top bottles. Population growth was initiated by pipetting 2 mL of *P. aurelia*

stock culture (~525 individuals/mL) into each microcosm. Microcosms were then randomly assigned to one of 30 experimental metapopulations, each comprised of two identical sink subpopulations.

Autocorrelated stochastic temperature fluctuations

Variable environments were created using a two-state Markov chain model of temperature fluctuations (Caswell and Cohen 1995, Gonzalez and Holt 2002). The temperature experienced by a population at any one time was in one of two states: 4°C or 18°C. The following transition matrix governed the fluctuations in temperature:

$$T = \begin{pmatrix} 1 - \lambda & \lambda \\ \lambda & 1 - \lambda \end{pmatrix}$$

where $0 < \lambda < 1$ and λ is the probability of a change in state. When $0 < \lambda < 0.5$, the fluctuations are positively autocorrelated and when $\lambda = 0.5$, the fluctuations are uncorrelated. Below we use the terms red and white to designate autocorrelated and uncorrelated fluctuation treatments, respectively.

For this experiment we generated 18 50-d temperature series (one change in temperature per day; Fig. 1), nine autocorrelated red series ($\lambda = 0.2$), and nine uncorrelated white series ($\lambda = 0.5$). All series consisted of 25 days at 4°C and 25 days at 18°C, resulting in equal means (11°C) and variances (50) across series, with the only difference being their autocorrelation structure.

Experimental design

The experiment included three crossed factors (spatial correlation, temporal autocorrelation, and dispersal), resulting in eight treatments with three replicates each. Metapopulations were designated as either spatially correlated (C; both subpopulations experienced the same temperature series) or spatially uncorrelated (U; each subpopulation experienced a different temperature series). Additional treatments included the autocorrelation structure of the temperature series [red (R) vs. white (W)] and the presence or absence of dispersal between sink subpopulations [dispersal (D) vs. no dispersal (N)]; from this point on we will use the term “metapopulation” as convenient shorthand to describe the paired sink populations not connected by dispersal. Thus, there were a total of eight treatment groups, denoted CRD, CRN, URD, URN, CWD, CWN, UWD, and UWN. In addition there were two 4°C control treatments, denoted CoD and CoN.

To ensure that the results were not biased by the unique properties of individual temperature series, a different randomly generated series was assigned to each replicate metapopulation in a treatment group. In the spatially uncorrelated treatments, six different series were used, one for each individual subpopulation, whilst in the spatially correlated treatments each subpopulation within a metapopulation experienced the same temperature series. Thus, three different series were used

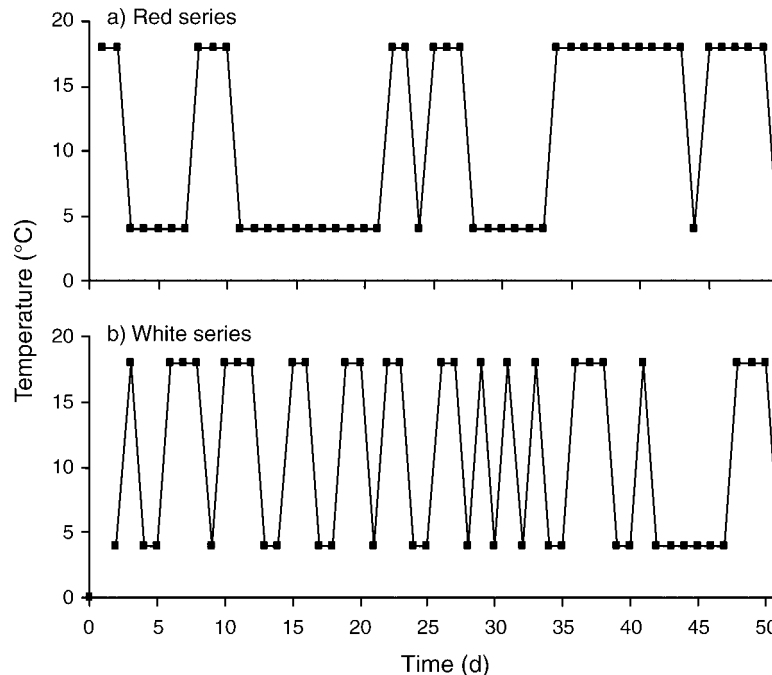


FIG. 1. Sample (a) autocorrelated red ($\lambda = 0.2$) and (b) uncorrelated white ($\lambda = 0.5$) temperature series used in the experiment. Both series have the same mean and variance (see *Materials and Methods: Autocorrelated stochastic temperature fluctuations*).

in each correlated treatment, one for each of the three replicate metapopulations. To allow for comparisons across dispersal treatments, the same series were used in both dispersal and nondispersal treatments.

It has been previously established that this strain of *P. aurelia* has slightly positive growth at 4°C (0.01 ± 0.02 cell divisions/d [mean \pm SE]; D. P. Matthews, *personal observation*). Thus microcosms at 4°C cannot be considered true sink habitats (i.e., negative growth rate). To establish weak sink conditions, 20 mL of medium was removed from each microcosm every two days (dilution rate of 0.2 d^{-1}) and replaced by 20 mL of sterile, non-bacterized, nutrient medium; this is standard protocol for semicontinuous cultures. From pilot experiments we established that growth rates in the presence of this dilution rate to be -0.61 ± 0.10 cell divisions/d at 4°C and 0.43 ± 0.03 cell divisions/d at 18°C. Because growth rate is linearly related to temperature between 4°C and 18°C (Gonzalez 1998) we calculated the mean of these two values and estimated the mean growth rate at 11°C (the experimental mean temperature) to be -0.09 cell divisions/d in the presence of dilution. The addition of this density-independent mortality created weak ambient sink conditions throughout the experiment, as required by the theory we tested.

After the initial bacterial inoculation and addition of *P. aurelia*, all experimental metapopulations were treated as closed systems. To simulate stochastic dispersal within the metapopulations, a 5-mL sample of nutrient medium was removed from each subpopu-

lation, and these two samples were then combined together in a sterile Petri dish. After gentle swirling, 5 mL of the combined sample was returned to each subpopulation. This process was repeated daily for groups receiving dispersal treatments, resulting in a net dispersal rate of 0.1 d^{-1} . On days when dilution was also performed, dispersal samples were removed from the subpopulations just before dilution. However, combined samples were not returned to the subpopulations until after the dilution treatment was complete. This ensured that the rate of dispersal remained constant from day to day. Rates of dilution remained constant for dispersal and nondispersal treatments because when dispersal occurred the same volume was removed and replaced with sterile medium in the nondispersal treatments.

Throughout the experiment, microcosms were kept in the dark in one of two temperature-controlled incubators, one maintained at a constant temperature of 4°C and one at a constant temperature of 18°C. Temperature fluctuations were simulated by moving the microcosms between the two incubators as dictated by the temperature series.

Population density

The population density of *P. aurelia* was estimated every two days for the duration of the experiment. Samples were taken just before dispersal and dilution. Before sampling, the bottles were gently swirled to produce an even cell distribution in the water column. A 1-mL sample was then removed from each microcosm using a sterile micropipetter and distributed as 10 drops

on a Petri dish. After sampling, 1 mL of sterile, nonbacterized nutrient medium was added to each microcosm, ensuring constant volume. The number of *P. aurelia* in each dish was counted using a stereomicroscope, and samples were diluted (1:10) before counting when necessary. Subpopulations were declared extinct after three consecutive counts (i.e., over 6 d) of 0 individuals/mL. This definition reliably defines a population as extinct when there is a consistent (as opposed to a fluctuating) trend to extinction, which was most often the case in this study.

Statistical analyses

We estimated the realized arithmetic growth rate r_t at day t from the mean number of cell divisions of *P. aurelia* per day, calculated as follows (see Gonzalez and Holt 2002):

$$N_{t+1} = N_t \times 2^{r_t}$$

giving

$$r_t = \log_2 N_{t+1} - \log_2 N_t.$$

The time-averaged arithmetic mean growth rate and maximum growth rate were then calculated for each subpopulation. It should be noted that this value is not exactly equal to the actual rate of cell division due to the effects of immigration and emigration.

To estimate the synchrony between the two populations of each metapopulation we used the intraclass correlation coefficient, r_i (Zar 1999; e.g., Rusak et al. 1999, Fontaine and Gonzalez 2005). When population fluctuations become increasingly synchronous, r_i approaches 1. If populations become asynchronous, then the correlation becomes negative. The intraclass correlation coefficient assumes samples are drawn from a normal distribution with equal variances; we thus normalized the counts by log transformation (Zar 1999). We calculated the intraclass correlation coefficient for each metapopulation over the duration of the experiment.

To directly address the hypothesized mechanism allowing sink–sink persistence (see Roy et al. 2005) we calculated spatial and temporal covariance between growth rates and population densities. A single spatial and temporal growth–density covariance value was calculated for each replicate metapopulation that persisted for at least 20 counts. This ensured maximum replication (three values) for subsequent analysis of variance.

Statistical differences in the mean density and maximum density, intraclass correlation, temporal and spatial growth rate–density covariance, and mean growth rate between treatment groups were tested using general linear models. For each of these variables we took the arithmetic mean of the two subpopulations in part because the true unit of replication was the metapopulation, but also because metapopulation persistence in a stochastic environment in the presence of

dispersal requires that the arithmetic mean growth rate across patches be greater than one (Roy et al. 2005). Because our measure of population synchrony, the intraclass correlation coefficient (r_i), is bounded between -1 and 1 , its distribution is not normal. To correct for this we transformed the r_i values using Fisher's z transformation (Zar 1999) before analysis of variance. In some instances certain values with large residuals were removed to check the model. In no instance did this qualitatively alter the final model, and we present here the results from the analysis of the complete data set. We report general linear models that contain only significant factors. These were obtained by a stepwise deletion of nonsignificant factors from the full model, i.e., main effects and their three- and two-way interaction terms. To meet model assumptions we tested homogeneity of variances, using Levene's test, before performing any analysis. A log or square-root transformation typically corrected for overdispersion. All analyses of variance were performed in SPSS (version 12; SPSS, Chicago, Illinois, USA). For the variable maximum density no transformation corrected for overdispersion. We performed an analysis of deviance in R (R Foundation for Statistical Computing, Vienna, Austria) using the quasipoisson errors to provide an ad hoc adjustment for overdispersion (Venables and Ripley 2002).

RESULTS

Metapopulation persistence was significantly altered by the presence of temperature fluctuations, spatial correlation in the temperature fluctuations, and dispersal between subpopulations (Fig. 2). Extinction of the sink metapopulations (summarized in Table 1) was expected in the constant environments, with or without dispersal, and indeed all six control metapopulations (with and without dispersal) went extinct during the course of the experiment. Extinctions of at least one, and sometimes both, subpopulations were observed in other treatments, supporting the prediction that environmental fluctuations alone do not ensure persistence. The only treatments in which all metapopulations persisted were the spatially uncorrelated red, with dispersal (URD) and the spatially uncorrelated white, with dispersal (UWD).

Realized metapopulation growth rates were significantly affected by the spatial correlation and dispersal treatments (Table 1, Fig. 3a). Arithmetic mean growth rates were significantly less negative in spatially uncorrelated metapopulations ($F_{1,21} = 10.05$, $P = 0.005$). Realized metapopulation growth rates were also less negative in the presence of dispersal ($F_{1,21} = 6.25$, $P = 0.02$). Growth rates were positive in the uncorrelated red with dispersal treatments (URD, 0.08 ± 0.03 cell divisions/d vs. URN, -0.05 ± 0.17 cell divisions/d) and uncorrelated white with dispersal treatments (UWD, 0.07 ± 0.02 cell divisions/d vs. UWN, -0.23 ± 0.29 cell divisions/d).

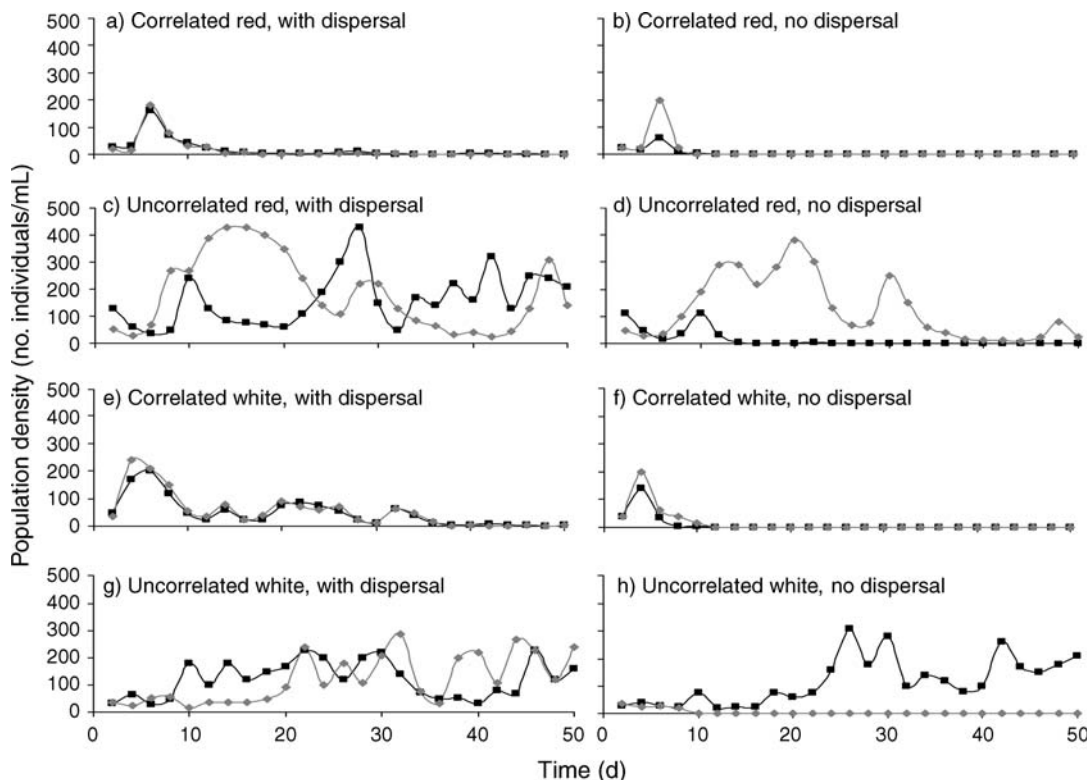


FIG. 2. Densities of *Paramecium aurelia* under different temperature and dispersal regimes as described in *Materials and Methods: Experimental design*. Graphs represent one sample metapopulation from each treatment group with both subpopulations plotted (gray and black lines).

As predicted, mean metapopulation densities were significantly affected by temporal autocorrelation, spatial correlation, and dispersal treatments (Fig. 3b). There were no significant interactions between these treatments. Mean metapopulation densities were 1.6 times greater (96 vs. 60 individuals/mL) in the presence of temporal autocorrelation ($F_{1,20} = 4.98$, $P = 0.037$); mean densities were four times greater (130 vs. 32 individuals/mL) when temperature fluctuations were spatially uncorrelated ($F_{1,20} = 49.9$, $P = 0.001$) and were almost doubled (101 vs. 55 individuals/mL) when dispersal was present ($F_{1,20} = 9.28$, $P = 0.006$).

Maximum population density was significantly affected by the temporal autocorrelation and spatial correlation treatments (Fig. 3c). There were no significant interaction terms. The maximum density was increased 1.5-fold (234 vs. 359 individuals/mL) by temporal autocorrelation in the temperature fluctuations (analysis of deviance, $t = 2.29$, $P = 0.03$) and 1.5-fold (243 vs. 361 individuals/mL) in spatially uncorrelated temperature fluctuations (analysis of deviance, $t = 2.12$, $P = 0.046$). There was no significant statistical effect of dispersal on maximum densities.

Spatial correlation and dispersal significantly affected population synchrony within the metapopulations, but there was no significant interaction between these two treatments (Fig. 3d). The correlation coefficient was

almost 10-fold greater (0.09 vs. 0.85) under spatially correlated temperature fluctuations ($F_{1,20} = 49.66$, $P < 0.001$) and two-fold greater (0.36 vs. 0.60) in the presence of dispersal ($F_{1,20} = 3.47$, $P = 0.07$). There was no effect of autocorrelation in temperature fluctuations on synchrony.

Time series of sufficient length to test for treatment effects on spatial and temporal growth–density covariances were obtained from the URD, UWD, CRD, and CWD series. Temporal growth–density covariance was significantly affected by the autocorrelation treatment ($F_{2,10} = 12.35$, $P = 0.002$), but not by spatial correlation. In temporally uncorrelated treatments mean temporal growth–density covariance was negative (-0.27 ± 0.04), while in temporally autocorrelated treatments mean temporal growth–density covariance was weakly positive (0.04 ± 0.07). Spatial growth–density covariance was significantly affected by spatial autocorrelation ($F_{2,10} = 44.4$, $P < 0.001$), although there was no effect of autocorrelation. In spatially uncorrelated treatments mean spatial growth–density covariance was 11 times greater (19.95 ± 3.0 vs. 1.75 ± 0.42) than in spatially correlated treatments.

DISCUSSION

There is mounting evidence that spatial and temporal fluctuations critically affect the dynamics of single

TABLE 1. Summary statistics with means for replicate sink metapopulations calculated over the duration of the experiment.

| Treatment and replicate | Maximum density (individuals/mL) | Arithmetic mean density (individuals/mL) | Metapopulation mean r (no. divisions/d) | Correlation coefficient | Extinctions per replicate metapopulation |
|-------------------------|----------------------------------|--|---|-------------------------|--|
| CRD | | | | | |
| 1 | 570.0 | 91.7 | -0.25 | 0.93 | 0 |
| 2 | 150.0 | 28.3 | -0.20 | 0.83 | 0 |
| 3 | 170.0 | 16.1 | -0.26 | 0.87 | 2 |
| Mean | 296.7 | 45.4 | -0.24 | 0.87 | 2 |
| CWD | | | | | |
| 1 | 220.0 | 50.1 | -0.22 | 0.92 | 0 |
| 2 | 245.0 | 24.9 | -0.26 | 0.87 | 0 |
| 3 | 210.0 | 45.5 | 0.04 | 0.89 | 2 |
| Mean | 225.0 | 40.2 | -0.15 | 0.89 | 2 |
| URD | | | | | |
| 1 | 430.0 | 172.4 | 0.04 | -0.15 | 0 |
| 2 | 410.0 | 162.3 | 0.06 | 0.55 | 0 |
| 3 | 645.0 | 245.9 | 0.14 | 0.64 | 0 |
| Mean | 495.0 | 193.5 | 0.08 | 0.35 | 0 |
| UWD | | | | | |
| 1 | 260.0 | 122.3 | 0.11 | 0.20 | 0 |
| 2 | 355.0 | 139.0 | 0.05 | 0.07 | 0 |
| 3 | 320.0 | 117.3 | 0.06 | 0.58 | 0 |
| Mean | 311.7 | 126.2 | 0.07 | 0.29 | 0 |
| CoD | | | | | |
| 1 | 20.0 | 2.2 | -0.68 | 0.83 | 2 |
| 2 | 24.0 | 2.3 | -0.63 | 0.75 | 2 |
| 3 | 26.5 | 2.6 | -0.61 | 0.73 | 2 |
| Mean | 23.5 | 2.4 | -0.64 | 0.77 | 6 |
| CRN | | | | | |
| 1 | 535.0 | 63.2 | -0.30 | 0.97 | 1 |
| 2 | 155.0 | 16.1 | -0.27 | 0.87 | 1 |
| 3 | 130.0 | 7.7 | -1.01 | 0.78 | 2 |
| Mean | 273.3 | 29.0 | -0.53 | 0.87 | 4 |
| CWN | | | | | |
| 1 | 170.0 | 11.6 | -1.07 | 0.48 | 2 |
| 2 | 200.0 | 14.8 | -0.02 | 0.89 | 2 |
| 3 | 155.0 | 12.6 | -0.50 | 0.89 | 2 |
| Mean | 175.0 | 13.0 | -0.53 | 0.75 | 6 |
| URN | | | | | |
| 1 | 245.0 | 69.5 | -0.39 | -0.72 | 0 |
| 2 | 335.0 | 103.3 | 0.06 | 0.19 | 0 |
| 3 | 530.0 | 172.2 | 0.18 | 0.39 | 1 |
| Mean | 370.0 | 115.0 | -0.05 | -0.05 | 1 |
| UWN | | | | | |
| 1 | 172.0 | 60.5 | -0.57 | -0.63 | 1 |
| 2 | ... | ... | ... | ... | ... |
| 3 | 271.5 | 70.3 | 0.01 | -0.10 | 0 |
| Mean | 245.4 | 74.8 | -0.23 | -0.37 | 1 |
| CoN | | | | | |
| 1 | 16.5 | 1.6 | -0.67 | 0.80 | 2 |
| 2 | 16.5 | 1.6 | -0.53 | 0.74 | 2 |
| 3 | 21.5 | 1.7 | -0.78 | 0.85 | 2 |
| Mean | 18.2 | 1.6 | -0.66 | 0.80 | 6 |

Notes: Abbreviations are: C, correlated; U, uncorrelated; R, red; W, white; D, dispersal; N, no dispersal; Co, control (see *Materials and Methods: Experimental design* for further details). We give the number of population extinctions occurring in each replicate metapopulation (1 or 2) and the total number of population extinctions across the three replicate metapopulations (maximum of 6) in each treatment. Ellipses indicate missing replicates.

species and multispecies source-sink systems (Virgí and Messier 2000, Loreau et al. 2003). Our results support the theoretical predictions of recent work (Jansen and Yoshimura 1998, Roy et al. 2005) and demonstrate that it is indeed possible for a metapopulation comprised

entirely of sink populations (on average) to persist in a stochastic environment. We have shown that dispersal and low spatial synchrony, enhanced by autocorrelated temporal variation in growth, can increase mean population densities, generate outbreak dynamics, and

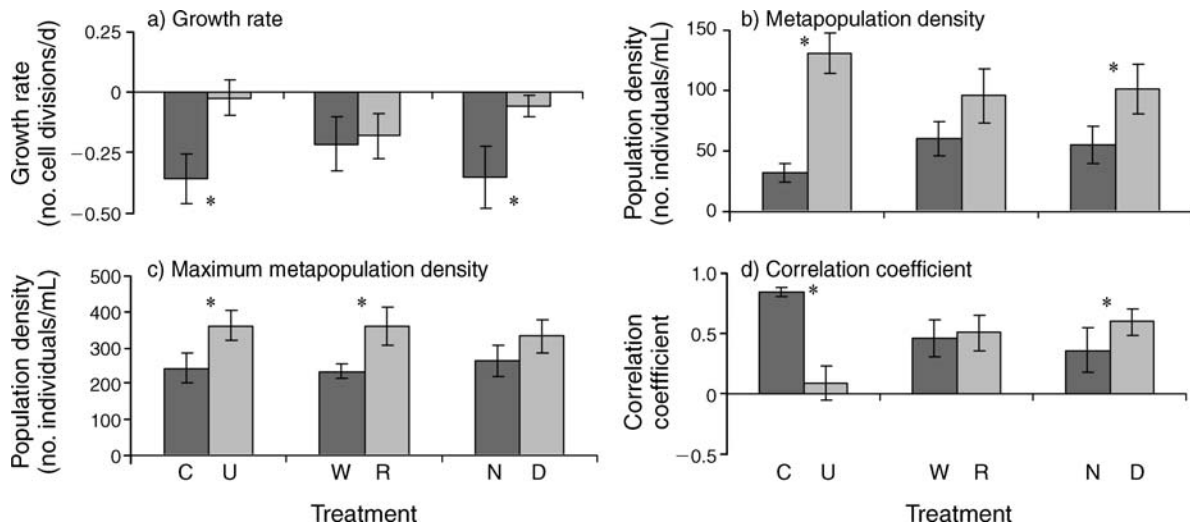


FIG. 3. Differences in (a) mean growth rate, (b) mean metapopulation density, (c) maximum metapopulation density, and (d) correlation coefficient. The panels compare correlated (C) to uncorrelated (U), white (W) to red (R), and no dispersal (N) to dispersal (D) treatments as described in *Materials and methods: Experimental design*. Asterisks indicate significance at $P < 0.05$; error bars are \pm SE.

allow for long-term sink metapopulation persistence. Positive temporal autocorrelation in growth produced greater mean and maximum densities, confirming that the inflationary effects of autocorrelation in source-sink systems previously reported by Gonzalez and Holt (2002) can be extended to sink-sink metapopulations (Roy et al. 2005). The ubiquity of autocorrelated environmental variation, both abiotic (Vasseur and Yodzis 2004) and biotic (Inchausti and Halley 2001), would suggest this is a result of broad relevance for our understanding of population and metapopulation persistence in habitats of low or deteriorating quality.

The results indicate that we successfully established the necessary experimental conditions to investigate the predictions of Roy et al. (2005). Temperature fluctuations coupled with dilution created ambient sink conditions in all treatment groups. As predicted by theory, we obtained long-term persistence (no extinction) of sink metapopulations in the presence of dispersal and spatially uncorrelated fluctuations in both red and white environments. These sink metapopulations were persistent because they were the only treatments that had an average spatial growth rate greater than zero (Table 1). The basic criterion for sink metapopulation persistence is an arithmetic mean growth rate across space greater than zero (greater than one in the discrete-time model of Roy et al. [2005]). According to theory, persistence is determined by the arithmetic mean in the presence of dispersal, whereas it is determined by the geometric mean in the absence of dispersal (Lewontin and Cohen 1969). Because the arithmetic mean is always greater than the geometric mean for any variable sequence of values it is possible to have an arithmetic mean greater than zero and a geometric mean less than zero. As Roy et al. (2005)

make clear, persistence in a sink metapopulation coupled by dispersal is influenced by a “cooperative” effect of asynchronous growth on all patches and positive spatial growth-density covariance; the spatial mean growth rate reflects this combined growth. Our experimental results provide a clear demonstration of this effect.

Roy et al. (2005) demonstrated that the inflationary effects of autocorrelated environmental variation are generated by positive temporal covariance between population densities and growth rates. We found autocorrelation in temperature resulted in weakly positive temporal growth-density covariance and greater mean and maximum densities (Table 1), whilst in uncorrelated environments temporal growth-density covariance was negative. Other calculations, not presented here, showed that greater mean and maximum densities were associated with positive autocorrelation in growth rates of the replicate populations (A. Gonzalez and D. P. Matthews, *unpublished data*). Together these results identify those demographic mechanisms responsible for the inflationary effect reported by Roy et al. (2005) to be occurring also in these experimental populations.

The lower levels of extinction we observed in sink populations in autocorrelated environments is also of interest because it runs counter to the much-studied prediction of enhanced extinction risk with increasing environmental autocorrelation in closed populations with positive long-term growth rates (Turelli 1977, Tuljapourkar 1982, Rotenberg 1987, Foley 1994, Johnst and Wissel 1997, Petchey et al. 1997, Pike et al. 2004, Tuljapourkar and Haridas 2006). Further experiments and theory comparing the effects of autocorrelated

environments on extinction risk in open and closed populations would be worthwhile.

Previous theory has shown that metapopulation persistence is hindered by population synchrony (e.g., Heino et al. 1997). The Moran effect suggests that metapopulation synchrony may be generated by spatial correlation in environmental conditions (Moran 1953), especially if populations share the same density-dependent structure. High levels of dispersal between local populations may also lead to metapopulation synchrony (Earn et al. 2000). Our results confirm the importance of these two effects. The mean intraclass correlation coefficient (our measure of synchrony) was almost 10-fold greater when temperature fluctuations were spatially correlated. The presence of dispersal (0.1 individuals/d) had a weaker effect but still almost doubled the level of synchrony in these sink metapopulations. These conclusions are supported further by the fact that more metapopulation extinctions occurred in the spatially correlated environments in the absence of dispersal than in its presence (Table 1). Experimental results of this kind are still few (Benton et al. 2001, Fontaine and Gonzalez 2005), but all are consistent with theory and suggest that low population synchrony is a fundamental property of persistent metapopulations, especially when composed of sink populations.

To maximize replication and explore as many aspects of the theory as possible we created metapopulations with only two subpopulations. This is a particularly stringent test of the theory developed by Roy et al. (2005) because, with the exception of perfectly correlated population fluctuations, the persistence of sink metapopulations becomes easier as the number of component populations increases. This is because increasing the number of subpopulations ensures that there is always a transient source population somewhere in the metapopulation. The strong relation between theory and experiment with only two subpopulations makes these results particularly compelling. Future experiments are required to investigate the effects of metapopulation size.

Our results reinforce the existing empirical and theoretical evidence for the inflationary effect of environmental variability (Gonzalez and Holt 2002, Holt et al. 2003, Roy et al. 2005). It has become increasingly clear that positive temporal autocorrelation has a strong influence on population abundance and persistence in both source-sink and sink metapopulation systems. While Pulliam's (1988) original model of source-sink dynamics is powerful in its simplicity and clarity, our evidence suggests that it must be extended to better account for spatial and temporal variability (e.g., Pulliam 2000, Loreau et al. 2003). The inflationary effect is the dynamical outcome of the interaction between dispersal and a stochastic environment that, if sufficiently autocorrelated, can be exploited by a sink population to achieve intermittent periods of growth and high abundance, ultimately lowering extinction risk.

In the context of a metapopulation this suggests that an ensemble of sink habitats may persist for long periods of time. This insight is consistent with the observation that additional understanding of metapopulation dynamics can be attained when within-patch population dynamics are taken into account (Hanski 1999).

When taken in conjunction with the theoretical work of Roy et al. (2005), our experimental results have broad implications for our understanding of species persistence in heterogeneous and deteriorating landscapes (Schiegg 2003). For example, these findings suggest that weak sink populations found at the edge of a species' range should show highly variable "outbreak" dynamics (Mehlman 1997). These dynamics may become more evident under the influence of anthropogenic climate change, which is believed to show increasingly autocorrelated fluctuations (Wigley et al. 1998). Further work in this area promises to expand our understanding of the role of dispersal and environmental fluctuations as determinants of population persistence and, from a conservation point of view, the dynamic effects of lowering population connectivity and lowering habitat quality in fragmented landscapes (Gonzalez et al. 1998, Earn et al. 2000).

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