

LETTER

The effects of immigration and environmental variability on the persistence of an inferior competitor

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Abstract

We tested the hypothesis that temporally autocorrelated variation should increase the abundance of an inferior competitor sustained by immigration. Temporally autocorrelated variability can increase abundance of the inferior species through effects on demography, the strength of competition, and the mean and variance in the abundance of competing species. We allowed the competitive inferior to immigrate into habitats with constant, variable, or temporally autocorrelated temperature regimes. In the absence of immigration, competitive exclusion occurred, in both constant and variable environments. Immigration permitted persistence of the inferior species, and increased immigration rates led to increased abundance. Temporally autocorrelated variability enhanced this effect of immigration. This ‘inflationary’ effect suggests that the interplay of immigration and environmental variability can jointly influence the outcome of competitive interactions. Our results suggest that an increase in temporal autocorrelation of environmental variability will cause regional processes to increasingly influence local interactions.

Keywords

Autocorrelated variability, coexistence, *Colpidium striatum*, competition, environmental colour, immigration, inflationary effect, metacommunity, temporal variability, *Tetrahymena thermophila*.

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INTRODUCTION

Understanding species coexistence in the face of competition for limiting resources is a central and abiding goal of community ecology (Hardin 1960; Hutchinson 1961; MacArthur & Levins 1967; Levin 1970; Armstrong & McGehee 1980; Chesson 2000). Theoretical studies in recent years have clarified the key role of spatial processes (such as dispersal) and temporal variability in influencing competitive coexistence (Holt & Barfield 2003; Snyder & Chesson 2004; Roy *et al.* 2005). An understanding of how spatial flows and temporal variability of the environment interact to govern coexistence in local communities is of vital practical importance, given the disruption of connectivity caused by anthropogenic landscape modifications and the looming threat of climate change. In this paper, we present results from an experimental microcosm suggesting that the interplay of immigration and temporal variability can

strongly affect the outcome of local interspecific interactions.

In open systems, immigration of an inferior competitor can allow that species to persist in habitats where, on average, it is declining to extinction (Shmida & Ellner 1984; Holt 1985; Pulliam 1988; Danielson 1991; Holt 1993; Dias 1996; Loreau & DeAngelis 1997; Diffendorfer 1998). With recurrent immigration, the abundance of an inferior competitor reflects a balance between its rates of immigration and competitive exclusion (Holt 1993, 2004). In a constant environment, the equilibrium abundance of the inferior competitor increases with the rate of immigration, and decreases with the absolute value of the rate of population decline.

This mechanism for local coexistence clearly does not require temporal variation (since it assumes a refuge from competition exists for the subordinate species), but temporal variation can influence the abundance of the

competitively inferior species. In the absence of immigration, the per capita growth rate of a competitively inferior competitor when rare is approximately

$$\left(\frac{1}{N}\right)\left(\frac{dN}{dt}\right) = r(t) = r_0(t) - \alpha(t)N'(t), \quad (1)$$

where $r_0(t)$ is the intrinsic growth rate of the focal species, N its abundance, $N'(t)$ the abundance of the resident dominant competitor, and $\alpha(t)$ the per capita strength of competition. The total impact of competition is $\alpha(t)N'(t)$. Temporal variation in the environment can potentially generate variation in (1) intrinsic growth rates, (2) the abundance of the competitor, or (3) the per capita strength of competition. Therefore, if a resident competitor exhibits fluctuations in abundance, this in turn generates temporal variation in the net strength of competition experienced by an inferior competitor (Roy *et al.* 2005). Environmental fluctuations that are positively autocorrelated can generate fluctuations in population size that are also positively autocorrelated, particularly for species that can closely 'track' their environments. Even white-noise variation can generate a positive autocorrelation in a species' abundance (Roughgarden 1975). Thus, one might often expect positive temporal autocorrelation in the intensity of competition, and therefore a positive autocorrelation in growth rate experienced by competitively inferior species.

In a temporally variable environment where a population is, on average, declining to extinction, but maintained by immigration, such a positive autocorrelation in growth rate can substantially increase its average abundance. The mathematical justification for this claim is presented in detail elsewhere (Holt *et al.* 2003; Roy *et al.* 2005), but the essential idea can be understood as follows. In an environment where a species on average experiences negative growth rates due to competition, a closed population is expected to go extinct with probability one, even though with temporal variation there may be transient periods of positive growth (e.g. Lewontin & Cohen 1969). With a positive autocorrelation in growth rates, there will be runs of good years, and runs of bad years. This does not prevent extinction in closed populations. Recurrent immigration, however, permits a population to persist through the bad years, so it can immediately respond by growing during runs of good years. If density dependence is weak, populations can grow to high levels during these runs of good years (Gonzalez & Holt 2002). Averaging over good and bad times, one finds that time-averaged abundance is weighted upwards by the spikes of abundance that emerge during temporary phases of good conditions. Gonzalez & Holt (2002) demonstrated this 'inflationary' effect using experimental studies of a laboratory microcosm with a single species of protozoan. In these experiments, a sink habitat was created by combining low temperature (lowering cell

division rates) and dilution (imposing mortality from harvesting).

In many natural communities, a local habitat may be a sink for a species due to the presence of superior competitors. Immigration can allow an inferior competitor to persist locally when it would otherwise be competitively excluded. The above arguments (initially developed for single species without considering interspecific interactions) suggest that environmental variability could increase the average abundance of the immigrating inferior competitor, especially if this variation has a positive temporal autocorrelation. We assessed this hypothesis experimentally by imposing different patterns of environmental fluctuations on competing protozoan species in laboratory microcosms. We first quantified how environmental variation (in productivity and temperature) influenced the relative competitive abilities of two competing ciliate protozoan species – *Tetrahymena thermophila* Nanney and McCoy and *Colpidium striatum* Stokes. Understanding the natural history of these bacterivores permits prediction of competitive outcomes in different environmental conditions and immigration rates (Fig. 1). We tested these predictions by allowing the species to compete in constant environments at different temperatures and productivities without immigration, and found

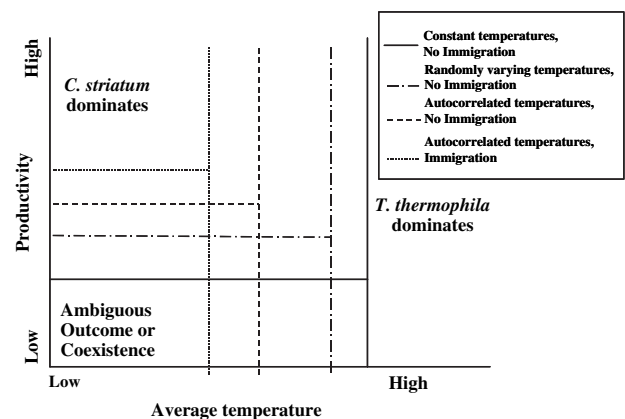


Figure 1 Hypothesized predictions of the outcome of competition between *Colpidium striatum* and *Tetrahymena thermophila* over varying productivities and temperature combinations. The four patterns of lines refer to how temperature varies (uncorrelated or autocorrelated changes) and whether *T. thermophila* could immigrate into the community. Each line pattern divides the graph into three areas that represent different outcomes of competition. These predictions are produced from observations of how the individual species respond to temperature and productivity. The four sets of lines symbolize a subset of the combinations of temperatures and productivities investigated in this experiment, and are meant only to suggest that *T. thermophila* will obtain higher abundances, and *C. striatum* will increasingly suffer, with decreasing productivity, increasing temperatures, increasing correlation between temperatures, and increasing immigration of *T. thermophila*.

that the outcome of competition was consistent with these predictions. We then evaluated how environmental variability and immigration of *T. thermophila* influenced its abundance in environments where, on average, *T. thermophila* would be competitively excluded by *C. striatum* in closed communities.

MATERIALS AND METHODS

Microcosm assembly and sampling

We used 260 mL covered glass bottles containing 100 mL of nutrient medium as our aquatic microcosms. Nutrient medium consisted of filtered well water, protozoan pellets (Carolina Biological Supply) as a source of nutrients for bacteria, and wheat seeds as an additional, slow-release carbon source. Both competing species are bacterivores. Previous work suggested that *C. striatum* dominates in many habitats, but that the strength of competition varies with productivity and temperature (Fox 2002). (Indeed, the name of *T. thermophila* suggest that it performs well at higher temperatures.) We inoculated 1.375 L of sterilized medium with four bacterium species (*Serratia marcescens*, *Bacillus subtilis*, *B. cereus*, and *Proteus vulgaris*) at least 4 days prior to adding either *C. striatum* or *T. thermophila* (obtained from Carolina Biological Supply). We allowed both protists to grow to high abundances in the 1.375 L flasks before dividing into microcosms consisting of 100 mL of the medium in 260 mL bottles. We initially grew the protists in this large batch culture rather than the 260 mL bottles to minimize differences in initial conditions. To estimate population density, we removed a small known volume (determined by mass with an electronic balance) of a thoroughly mixed microcosm and counted protists under a Nikon SMZ-U dissecting microscope. We diluted samples by weight if densities were too high to count in undiluted samples.

We manipulated both productivity and temperature. We controlled productivity by using different amounts of protozoan pellets and wheat seeds for the medium. Protozoan pellet concentration determines initial bacterial abundances (Kaunzinger & Morin 1998; Fox 2002). The high and low productivity treatments respectively contained 0.55 g L⁻¹ protozoan pellets and three wheat seeds, and 0.27 g L⁻¹ protozoan pellets and two wheat seeds. We used one additional productivity level (0.13 g L⁻¹ protozoan pellets and one wheat seed, referred to as 'lowest') in the 'Competition in constant environments' experiments described below. We manipulated temperature with programmable incubators (Percival I-6 VL with 982 microprocessors; Percival Scientific, Inc., Iowa, IA, USA) for all experiments except for the rate of exclusion experiment described below. For this experiment, we used water baths to manipulate temperature (incubators were unavailable).

Single species demography

We evaluated how each species' intrinsic rate of increase (r), carrying capacity (K), and competitive ability (R^*) varied with productivity and temperature. We measured the extent to which environmental variability can affect population densities by determining how well each species tracked varying temperatures. We measured r and K in all combinations of two productivities (low and high) and three constant temperatures (22 °, 27 ° and 32 °C) replicated three times, giving a total of 36 microcosms. We added a small initial number (< 4 individuals per 1 mL) of either *C. striatum* or *T. thermophila* to the six environments and monitored growth until populations reached equilibrium (determined by visual inspection of growth curves). We measured r as the slope of the regression of log (number of individuals per mL + 1) on time during the exponential growth phase, and K as mean population density once the population had reached equilibrium.

We measured competitive ability by assessing R^* (Tilman 1982), defined as the level to which each species reduces bacterial density at equilibrium. We assessed R^* in all combinations of two productivities (low and high) and three temperatures (22 °, 26 ° and 30 °C) replicated four times. Prior studies using these species have shown that the level to which a protist reduces bacteria measures that species' competitive ability (Fox 2002). We acknowledge that bacterial composition can change as the result of consumption, and that differences among species in their use of different bacteria could allow coexistence (Jiang & Morin 2005; Fox & Barreto 2006). However, we did find general correspondence between the R^* measure of competitive ability and species dominance. We measured bacterial abundance 10 days after establishing the monocultures (sufficient time for each species to reach its respective carrying capacity) using standard plate counting techniques. We tested if r , K and R^* of each species differed among environments with two-way ANOVAs (Proc GLM in SAS/STAT version 6.12), conducting separate analyses for each species.

The ability of a population to track environmental changes depends on how fast the environment changes relative to its r (May 1973; Roughgarden 1975). To evaluate the ability of *C. striatum* and *T. thermophila* to track environmental change, we grew three replicates per species in monoculture under four different fluctuating temperature regimes at both low and high productivity. We used 'spectral mimicry' (Cohen *et al.* 1999) to create two reddened (temporally autocorrelated) series and two white (temporally uncorrelated) series, to separate effects of colour from the effects of a particular series, and to avoid confounding colour with incubator identity. Mean, minimal, and maximal temperatures of each series were respectively 27 °, 22 ° and

32 °C. The temperatures used in the series were $22 + 10x/77$, where $x = 0, 1, 2, \dots, 77$. All four fluctuating temperature regimes contained the same 78 values for temperature, but the order in which temperatures occurred varied (as in the protocols of Petchey 2000 and Gonzalez & Holt 2002). Randomly shuffling the 78 temperatures created 'white series'. Rearranging these random series to create an autocorrelation between successive temperatures generated 'reddened series' with identical means and variances to the white series (see Fig. S1 in Supplementary material). At each time step, temperatures changed linearly (ramped) to the next value over a 12 h period. The experimental duration was designed to be 39 days. We uploaded the four temperature regimes to four programmable incubators using PACES software (Percival Scientific Inc., Iowa, IA, USA) installed on a PC. Temperatures were recorded every 15 min, and generally followed the temperatures prescribed by the programme. We evaluated each species' ability to track environmental changes using correlation coefficients between abundance and the mean temperature of the previous 48 h for each replicate for each species.

Competition in constant environments

We observed competitive outcomes between *C. striatum* and *T. thermophila* in nine different constant environments; the environments were defined by combinations of three productivities (lowest, low and high) and three temperatures (22 °, 27 ° and 32 °C). We grew each species in monoculture in a large batch (1.375 L) at the three productivity levels for 10 days. We then initiated the competition experiments by adding 50 mL from the monoculture batch of each species to the same microcosm, at each productivity level. Thus, microcosms ultimately contained 100 mL of medium; the initial densities (mL^{-1}) of each species were related to each species carrying capacity, leading to initial densities of *c.* 194 *C. striatum* and 65 *T. thermophila* at high productivity, 114 *C. striatum* mL^{-1} and 114 *T. thermophila* mL^{-1} at low productivity, and 54 *C. striatum* mL^{-1} and 54 *T. thermophila* mL^{-1} at the lowest productivity. In this system, the long-term outcome of competition generally appears to be largely independent of initial densities when species compete exclusively for bacteria (Long & Karel 2002). Three microcosms from each productivity were placed in 22 °, 27 ° or 32 °C water baths. We monitored densities of both species for 25 days (≥ 25 generations).

Effects of immigration and environmental variability on competitive interactions

To determine effects of immigration and environmental variability on competitive interactions we crossed three levels of immigration (none, low and high) with six

temperature regimes (constant 22 °C, constant 27 °C, two reddened series, two white series; the latter series are those described above (Fig. S1 in Supplementary material)). We initially conducted this experiment in a high productivity protist pellet medium, and then conducted the same experiment with the same temperature regimes in a low productivity medium. An optimal design would have been to conduct the high and low productivity experiments simultaneously, but this was logistically impossible, as this part of the experiment was conducted by one person (Z. Long). Additionally, we chose to immigrate *T. thermophila* in conditions where it was expected to be the competitive inferior, on average (all of the temporally variable series had an average temperature of 27 °C). Specifically, the experiments on species demography and in constant environments suggest that *T. thermophila* was the inferior competitor at 22 ° and 27 °C. A more complete design would have been to reciprocally immigrate *C. striatum* at higher temperatures or very low productivities where it was the competitive inferior. Logistics, again, prevented us from performing this additional set of treatments.

To start the experiment in high productivity, we combined *c.* 620 *C. striatum* mL^{-1} and 260 *T. thermophila* mL^{-1} in microcosms maintained in the constant 22 °C, constant 27 °C, and two white temperature regimes, and *c.* 435 *C. striatum* mL^{-1} and *c.* 215 *T. thermophila* mL^{-1} to the microcosms in the two reddened temperature series. To start the experiment at low productivity, we combined *c.* 130 *C. striatum* mL^{-1} and *c.* 120 *T. thermophila* mL^{-1} in microcosms for all temperature treatments.

We manipulated immigration as follows. We vigorously mixed the microcosms, then removed 10 mL of the medium with a sterile pipette, and then added either 10 mL of unfiltered medium from a 100 mL *T. thermophila* monoculture (high immigration; on average 10% of *K*), 1 mL unfiltered medium from a 100 mL *T. thermophila* monoculture plus 9 mL of filtered medium from that monoculture (low immigration; on average 1% of *K*), or 10 mL of filtered medium from a *T. thermophila* monoculture (no immigration). We filtered medium using a vacuum filter system and glass microfibre filters, which removed all *T. thermophila* (Z. Long, personal observation). We added immigrants at 2–4 day intervals. We replicated the 18 treatments (6 temperatures \times 3 immigration levels) three times. We established monocultures of *T. thermophila* weekly as described above to ensure a fresh and healthy source of *T. thermophila*, and to provide roughly similar numbers of immigrants per immigration event throughout the experiment. We maintained the monocultures in constant 27 °C environment (the mean temperature for all treatments but the constant 22 °C environment).

We monitored population densities at 3–4 day intervals as described above. We allowed at least 48 h (at least two

generations) after immigration to monitor population densities, except for once in the high productivity experiment (immigrated on day 30, counted on day 31). We used average density of each species over the course of the experiment to measure competitive outcomes. We assessed if immigration and the colour of the temperature series influenced average density with four two-way ANOVAs, one for each species in both productivity levels.

RESULTS

Single species demography

Temperature and productivity influenced r in both species (Fig. S2 in Supplementary Material). *Tetrabymena thermophila*'s r increased with temperature ($F_{2,17} = 83.86$, $P < 0.001$) and productivity ($F_{1,17} = 105.84$, $P < 0.001$). There was a significant interaction between temperature and productivity, likely due to the greater increase in r at 32 °C in low productivity relative to high productivity ($F_{2,17} = 11.81$, $P = 0.001$). *Colpidium striatum*'s r peaked at 27 °C ($F_{2,17} = 20.15$, $P < 0.001$) and increased with increasing productivity ($F_{1,17} = 23.64$, $P < 0.001$). There was a significant interaction between temperature and productivity, due to the greater decrease at 32 °C in low productivity relative to high productivity ($F_{2,17} = 11.36$, $P = 0.001$).

Temperature and productivity influenced K of both species (Fig. S2). *Tetrabymena thermophila*'s K peaked at 27 °C ($F_{2,17} = 6.92$, $P = 0.010$) and increased with increasing productivity ($F_{1,17} = 17.74$, $P = 0.001$). *Colpidium striatum*'s K varied with increasing temperature ($F_{2,17} = 3.89$, $P = 0.049$) and increased with increasing productivity ($F_{1,17} = 83.00$, $P < 0.001$). Neither species showed a significant interaction between temperature and productivity ($F_{2,17} = 1.02$, $P = 0.389$ for *T. thermophila*; $F_{2,17} = 2.97$, $P = 0.090$ for *C. striatum*).

Temperature and productivity influenced the competitive ability of both species (Fig. S2). *Tetrabymena thermophila*'s R^* decreased with increasing temperature ($F_{2,23} = 38.80$, $P < 0.001$) and decreasing productivity ($F_{1,23} = 24.41$, $P < 0.001$). There was a significant interaction between temperature and productivity ($F_{2,23} = 10.33$, $P = 0.001$). This interaction reflects the precipitous decline in R^* from 22 ° and 26 ° to 30 °C in high productivity treatments, while R^* steadily declined with temperature in low productivity treatments. The influence of temperature on *C. striatum*'s R^* showed essentially the opposite pattern as for *T. thermophila*. R^* for *C. striatum* increased with increasing temperature ($F_{2,21} = 5.38$, $P = 0.016$) and productivity ($F_{1,21} = 4.78$, $P = 0.044$). There was not a significant interaction between temperature and productivity ($F_{2,21} = 0.84$, $P = 0.450$). (No bacteria grew on two plates: one low productivity 30 °C replicate, and one high productivity

30 °C replicate. We disregarded these counts, which likely reflected idiosyncratic laboratory errors.)

Tetrabymena thermophila did not significantly differ in its ability to track reddened vs. white environments at low productivity (Fig. S3 in Supplementary Material, $F_{1,11} = 1.53$, $P = 0.245$), but did differentially track different thermal regimes at high productivity (Fig. S3, $F_{1,11} = 6.27$, $P = 0.031$). Abundance of *C. striatum* was more negatively correlated with temperature in reddened environments than white at both levels of productivity ($F_{1,11} = 17.54$, $P = 0.002$ for low productivity, $F_{1,11} = 6.87$, $P = 0.026$ for high productivity). The value of the correlations of *C. striatum* and *T. thermophila* in reddened environments differed in sign. These results, combined with r , K , and R^* , indicate that *C. striatum* suffered, while *T. thermophila* benefited, from increasing temperature and increased autocorrelation.

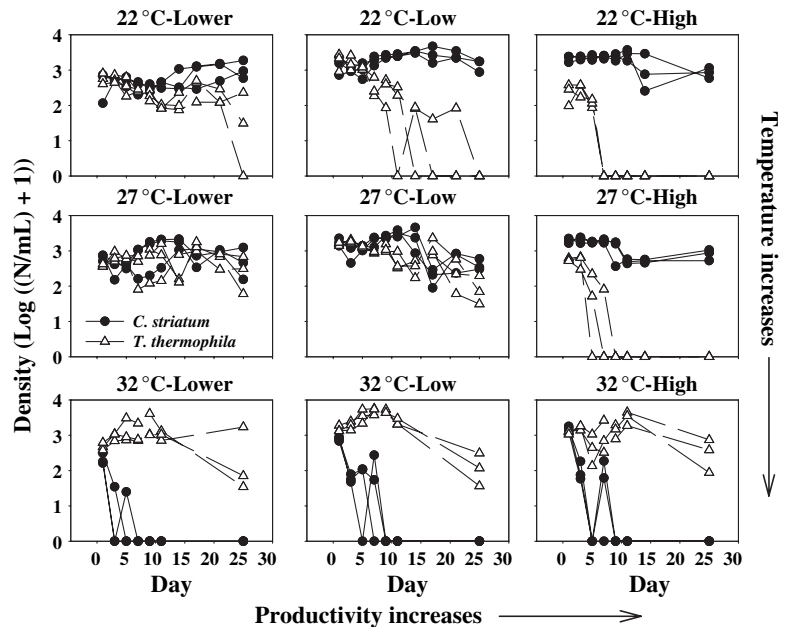
Competition in constant environments

As predicted from the above results, the outcome of competition between *C. striatum* and *T. thermophila* in the nine different constant environments varied (Fig. 2). Moreover, R^* s from constant environments can correctly predict the outcome of competition: *C. striatum* dominated at higher productivities, and *T. thermophila* dominated at higher temperatures. The outcome was somewhat ambiguous at lower temperatures (22 ° and 27 °C) and the lowest productivity, but *T. thermophila* began to decline after 25 days of competition, suggesting that long-term coexistence is unlikely (see Long 2004 for additional details).

Effects of immigration and environmental variability on competitive outcomes

Without immigration, *T. thermophila* went extinct, or was headed towards extinction, in all treatments (Figs 3–5). Immigration, environmental variability, and their interaction all significantly influenced the average density of *T. thermophila* in competition. In both productivities, the greatest average density of *T. thermophila* occurred in reddened environments, followed by white environments, followed by constant 27 °C, with the lowest average densities in constant 22 °C (separate ANOVAs for each productivity level: $F_{5,53} = 3.46$, $P = 0.011$ in low productivity; $F_{5,53} = 11.15$, $P < 0.001$ in high productivity, Fig. 6). Immigration increased the densities within each temperature condition (separate ANOVAs for each productivity level: $F_{2,53} = 573.14$, $P > 0.001$ in low productivity; $F_{2,53} = 196.62$, $P < 0.001$ in high productivity, Fig. 6). It is unclear why the interaction between temperature and immigration significantly influenced *T. thermophila* average density in low, but not high productivity (separate ANOVAs for each

Figure 2 Population dynamics of *Tetrahymena thermophila* (open triangles) and *Colpidium striatum* (filled circles) in competition in nine temporally constant environments. The nine environments are all possible combinations of three temperatures (22 °, 27 ° and 32 °C) and three levels of productivity (lowest, low and high). Productivity increases from the left panels (lowest productivity) to the right panels (highest productivity), and temperature increases from the top panels (22 °C) to the bottom panels (32 °C).



productivity level: $F_{10,53} = 3.99$, $P = 0.001$ in low productivity; $F_{10,53} = 1.23$, $P = 0.304$ in high productivity; Fig. 6).

Temperature influenced the density of *C. striatum* in competition. In both productivities, the greatest average density of *C. striatum* occurred in constant 22 °C, followed by constant 27 °C, followed by white environments, with the lowest average densities in reddened environments ($F_{5,53} = 42.84$, $P < 0.001$ for low productivity; $F_{5,53} = 40.99$, $P < 0.001$ for high productivity, Fig. 6). Immigration of *T. thermophila* did not influence the density of *C. striatum* at low productivity, but surprisingly increased the density of *C. striatum* at high productivity ($F_{2,53} = 0.05$, $P = 0.952$ for low productivity; $F_{2,53} = 10.68$, $P < 0.001$ for high productivity, Fig. 6). While the increase in *C. striatum* density was statistically significant, it should be noted that this effect was quite modest compared with temperature effects (Fig. 6; the effect size of temperature greatly exceeded the effect size of immigration; $\omega^2 = 0.06$ for immigration, $\omega^2 = 0.73$ for temperature). The interaction between temperature and immigration did not influence *C. striatum* density ($F_{10,53} = 0.20$, $P = 0.995$ for low productivity; $F_{10,53} = 1.07$, $P = 0.407$ for high; Fig. 6).

DISCUSSION

Theory predicts that a competitively inferior species can persist in a local patch if immigration from a persistent source of immigrants offsets losses due to competition (Holt 1993, 2004). Moreover, autocorrelated temporal variation can allow for periods of positive population growth in a patch that is, on average, a sink (Gonzalez &

Holt 2002). These prior studies have emphasized single-species dynamics, but comparable effects should arise when a sink emerges from competitive interactions. We found that recurrent immigration of a competitively inferior species allowed that species to persist in habitats where it otherwise is competitively excluded. Furthermore, temporally autocorrelated variability generated periods of negative population growth and reduced abundance for the competitively superior species. During these periods, the immigrating inferior species enjoyed phases of relaxed competition and rapid population growth, leading to higher abundances, on average, in temporally autocorrelated environments than in similar but constant environments.

Our experimental design assumed that rates of immigration of the inferior competitor are constant, while local growth rates vary through time. This is an analytically tractable limiting case which we suggest illuminates more complex scenarios. Moreover, it could literally describe some natural systems. We assumed that even though our focal species is competitively inferior in one habitat, there is another habitat (the source) where it is resident and persists. Strong density dependence in the source could buffer the effect of temporal variation on population size there; the source could stay near carrying capacity providing a roughly constant stream of immigrants into the sink. This scenario could also pertain to some applied ecological scenarios, such as augmentation in biological control or reintroduction schemes in conservation, where fixed immigration rates are set by management strategies. Nonetheless, we would be cautious in applying our findings literally to natural systems where immigration is likely also to vary through time. A task

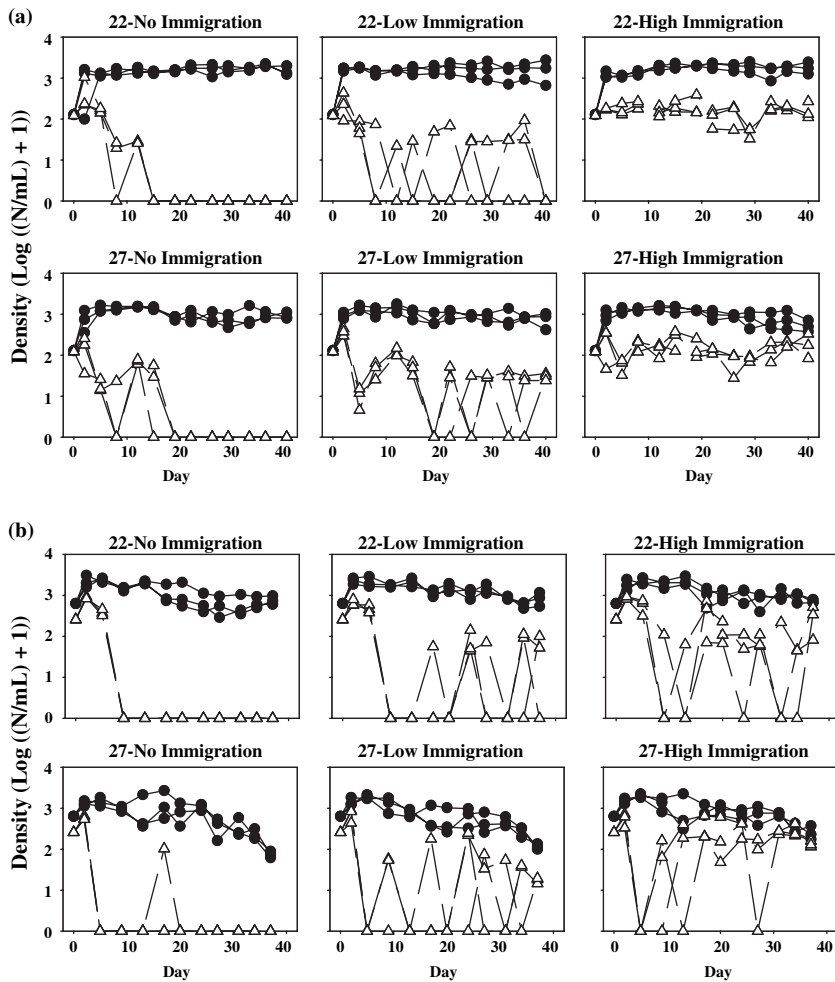


Figure 3 Population dynamics of *Tetrahymena thermophila* (open triangles) and *Colpidium striatum* (filled circles) in competition in constant 22 ° and 27 °C with three levels of immigration of *T. thermophila* (no immigration, low immigration and high immigration) at low productivity (a) and high productivity (b).

for future theoretical and experimental work will be to examine the interplay of dispersal and temporal variation in determining the outcome of competition across arrays of patches that exhibit both spatially and temporally autocorrelated variation (see Roy *et al.* 2005).

Single species demography

Temporal variability can permit coexistence or at least slow down competitive exclusion, if species respond differently to changes in environmental conditions (Hutchinson 1961; Levins 1979; Chesson & Case 1986). Our analyses of species demography in monoculture suggests that the growth rate and competitive ability of our two species respond differently to the environment. *Tetrahymena thermophila*'s growth rate increased with productivity and temperature, while *C. striatum*'s growth rate peaked at intermediate temperature. The competitive effect of *C. striatum* on *T. thermophila* also changed with environment; each species' R^* varied in opposing ways. *Tetrahymena thermophila*'s

competitive ability increased, while *C. striatum*'s decreased, with increasing temperatures.

Competition in constant environments

Matching these single-species growth responses, *C. striatum* generally dominated at higher productivities, *T. thermophila* dominated at higher temperatures, and the species coexisted (at least over the time scale of the study) at lower productivities and intermediate temperature. Transient coexistence at the lower productivities and middle temperature despite differences in R^* hints at complexities in the interactions between these species not captured by traditional theories of competition for a single shared resource. Prior studies of this system have shown that competitors can coexist despite differences in R^* ; dominant competitors do generally have lower R^* values, but they do not always exclude species with higher R^* values (Fox 2002; Fox & Barreto 2006). Fox & Barreto (2006) rejected several possible explanations for the long-term coexistence of

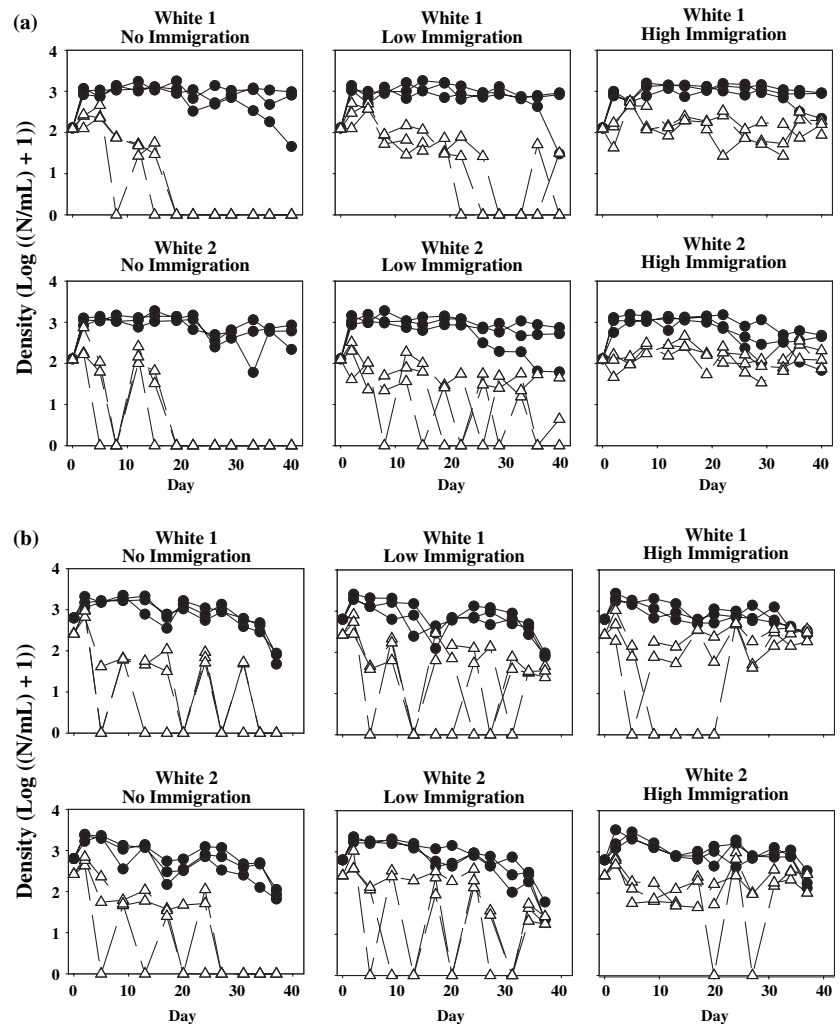


Figure 4 Population dynamics of *Tetrachyena thermophila* (open triangles) and *Colpidium striatum* (filled circles) in competition in temporally uncorrelated varying temperatures with three levels of immigration of *T. thermophila* (no immigration, low immigration and high immigration) at low productivity (a) and high productivity (b). The minimum, average and maximum temperatures were 22 °, 27 °, and 32 °C, respectively.

competing protists in closed environments, including chemical interference, effects of bacterial composition, and spatial segregation of competitors. A detailed mechanistic understanding of coexistence in this system is not yet developed (Fox & Barreto 2006).

Effects of immigration and environmental variability on competitive interactions

In open environments, both theory and the experimental results presented above show that immigration permits the persistence of an inferior competitor in constant environments; local coexistence reflects the presence of a competitive refuge elsewhere in the landscape (the source). In our experiments, temporal variation alone (either white or reddened) did not lead to coexistence. However, positively autocorrelated temporal variation magnified the effect of immigration upon the abundance of the inferior competitor. In effect, immigration ensures

the availability of propagules during transient runs of favourable conditions.

A number of specific effects could underlie the experimental effects we observed. Temporal variation could create favourable conditions for an inferior competitor via shifts in: (1) its density-independent growth components (r_0 in eqn 1), (2) per capita interaction strength ($\alpha(t)$ in eqn 1), (3) average abundance of the dominant competitor (N' in eqn 1), and (4) temporal variation in abundance of the dominant competitor. These four possibilities are not mutually exclusive. In future studies we hope to disentangle these effects in some detail, and here briefly discuss some qualitative indications of how these factors may be reflected in our experimental results.

The single-species results suggest that temporally autocorrelated variation in temperature produces temporally autocorrelated variation in r for both competitors. The two species appear to differ in their ability to track the environment. In white environments, both species appear

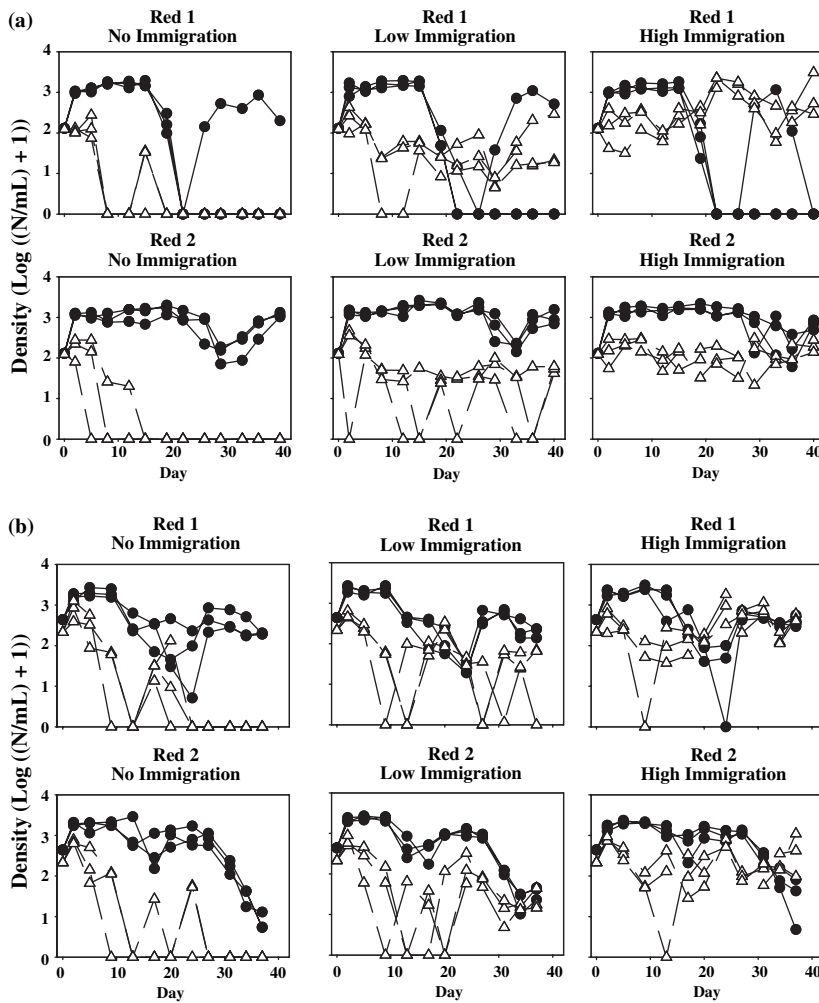


Figure 5 Population dynamics of *Tetrahymena thermophila* (open triangles) and *Colpidium striatum* (filled circles) in competition in temporally correlated varying temperatures with three levels of immigration of *T. thermophila* (no immigration, low immigration and high immigration) at low productivity (a) and high productivity (b). The minimum, average and maximum temperatures were 22 °, 27 °, and 32 °C, respectively.

to be slightly anti-tracking, so the inferior competitor may be able to experience the temperature at which it grows well with a lower than average density of the superior competitor. By contrast, in the red environment, the competitive dominant severely anti-tracks (Fig. S3), so the environments that are best for the growth of the inferior competitor coincide with periods of high density. These shifts in the covariance between the environment and competition can influence the overall impact of competition (Chesson 2000). Moreover, the strength of the competitive interaction may change with temperature, because the degree to which resources are utilized by both species depends on temperature. If competition is at least partially mediated through resources, temporally autocorrelated variation in consumption may generate temporally autocorrelated variation in per capita impacts of competitors. Thus, changes in either intrinsic demography affecting tracking ability, or in the strength of competitive interactions, could have played a role in increasing the abundance of the inferior competitor in reddened environments.

The strength of interspecific interactions experienced by inferior competitors depends on the abundance of the resident dominant competitor. The average effect of competition over time thus depends on how temporal autocorrelation influences the average abundance of the dominant competitor over time. We found that the average abundance of *C. striatum* was generally lower in red environments. The decrease in abundance of *C. striatum* could thus have lessened the average impact of competition, and so contributed to the increase in the average abundance of *T. thermophila* in reddened environments. We note that in the absence of immigration, during the transient phase of persistence before going extinct, *T. thermophila* reached its highest abundances in temporally variable environments. This suggests that environmental variation can have a positive effect on transient coexistence.

The effect of temporal variation in the dominant competitor's abundance on the average abundance of the subordinate over time resembles the inflationary effect discussed by Gonzalez & Holt (2002) and Holt *et al.* (2003).

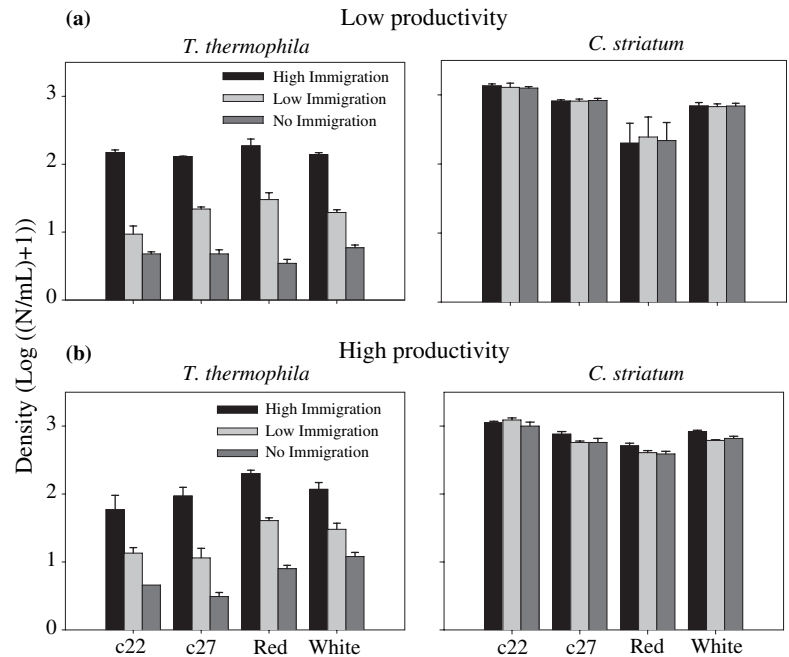


Figure 6 Mean density (± 1 SE) of *Colpidium striatum* in low (a) and *Tetrabymena thermophila* and high productivities (b) over the duration of competition in the different environments with immigration of *T. thermophila*.

They demonstrated that variation in a species' rate of exclusion generated by temporally autocorrelated environmental conditions could increase abundance in a sink habitat by allowing population outbreaks during runs of good conditions (Gonzalez & Holt 2002). In our system, variation in the abundance of the dominant competitor should imply variation in the realized rate of exclusion of the inferior competitor (i.e., the severity of the sink varied over time), and permit transient periods of population growth. Such variation can increase the time-averaged abundance of the inferior competitor, independent of direct effects on the subordinate's population parameters or shifts in the mean abundance of the resident dominant competitor.

In our study, effects of environmental variation on the abundance of the inferior competitor were much stronger in temporally autocorrelated environments than in comparably variable, but uncorrelated, environments. This supports the idea that the internal structure of environmental variation can determine when such variation appreciably impacts ecological processes (Leigh 1981; Goodman 1987; Lande 1993; Halley & Kunin 1999). Whether autocorrelated environmental variation leads to inflated abundances of a particular population (as observed with *T. thermophila*), or not, may depend on whether interacting species respond similarly to the environment. With competing species, if species respond differently to the environment (as in this experiment) autocorrelated environmental variation should lead to an increase in abundance of an inferior species that persists

because of immigration. By contrast, if competitors respond similarly to the environment, then autocorrelated environmental variation could hamper coexistence (Caswell & Cohen 1995).

Broader implications

Our results add to a growing list of studies that suggests the structure, or colour, of temporal variance plays an important role in determining community composition. Colour can influence extinction risks (Ripa & Lundberg 1996; Petchey *et al.* 1997; Heino 1998), population dynamics (Roughgarden 1975; Heino 1998; Morales 1999; Gonzalez & Holt 2002), predator-prey dynamics (Fontaine & Gonzalez 2005) and the coexistence of competitors (Caswell & Cohen 1995). Here, we have shown that temporally autocorrelated variation can influence competitive interactions and inflate the effect of immigration, leading to substantial average abundances for a competing inferior species maintained by immigration.

One poorly understood dimension of climate change may be a shift in the autocorrelation structure of temporal variation. If some species are locally abundant because of the interplay of immigration and temporal variability, they may be vulnerable to a collapse in abundance either because of the severing of connectivity between local habitats and a broader landscape, or because of shifts in the autocorrelation structure of the environment, even if the mean environment does not change. We suggest that

understanding the interplay of temporal variation and spatial flows is a significant challenge in both basic and applied ecology which warrants much more attention.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 The temperature series used in the experiments involving temperature manipulations.

Figure S2 Species traits in constant temperatures and productivities.

Figure S3 The ability of (a) *Tetrahymena thermophila* and (b) *Colpidium striatum* to track temporally autocorrelated (red) or temporally uncorrelated (white) temperatures in monoculture at two levels of productivity.

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