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Adaptive radiation in a fluctuating environment: disturbance affects the evolution of diversity in a bacterial microcosm

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ABSTRACT

Questions: How is adaptive radiation affected by disturbance? Does the temporal pattern of disturbance affect the rate of adaptive radiation?

Organism: The bacterium *Pseudomonas fluorescens* SBW25, which exhibits fast and repeatable adaptive radiation *in vitro*.

Experiments: We compared the dynamics of adaptive radiation over many generations in disturbed and undisturbed habitats. The disturbance was an abrupt homogenization of the liquid habitat. Habitats experienced either autocorrelated or uncorrelated disturbance.

Results: Disturbance significantly slowed divergence rates, and it did so more strongly when autocorrelated than when uncorrelated. Despite the slower diversification in the disturbed treatments, diversity converged to a similar steady state in all treatments by the end of each experiment.

Keywords: adaptive radiation, autocorrelation, disturbance, diversification, microbial microcosm, *Pseudomonas fluorescens*, species richness.

INTRODUCTION

The emergence of diversity within a rapidly growing population is a major evolutionary feature known as adaptive radiation. It occurs when a single ancestor diversifies to use a range of environments where each type differs in traits that are used to exploit those environments (Schluter, 2000). The principal explanations for this widespread phenomenon focus either on divergent selection generated by environmental heterogeneity both in space (Day, 2000) and time (Gibbs and Grant, 1987), or divergent selection generated by competition for limiting resources that drives closely related species to exploit different parts of a resource spectrum. Great progress has been made in our empirical and theoretical understanding of

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the workings of these processes (Schluter, 2000). However, much of our knowledge of adaptive radiation is limited to either controlled laboratory experiments in constant environments in which selection is considered to be continuous through time, or to studies of natural populations where the environment cannot easily be controlled. As a result, we know little about the effects of disturbance on adaptive radiation and in particular whether intermittent disturbance hinders or favours the process (Gotelli and Bossert, 1991; Schluter, 2000). Given the ubiquity of environmental disturbance across all scales of space and time, this is a surprising observation. To address this issue we studied the effects of disturbance upon the evolution of diversity in a microbial microcosm.

Following Gerritsen and Patten (1985), we define disturbance rather generally as an 'infrequent event or episode that causes a system to deviate from its expected or regular state'; this definition subsumes many of the previous uses of the term in the literature. The relationship between disturbance and the maintenance of diversity is a classical question in community ecology that has received considerable theoretical (e.g. Huston, 1994) and empirical attention (e.g. Buckling *et al.*, 2000; Kassen *et al.*, 2000). However, the effect of disturbance on the evolution of diversity has rarely been considered (Allmon *et al.*, 1998). To ascertain how disturbance causes a diversifying population to deviate from its expected trajectory, it is necessary to consider the type of disturbance and how it may influence the rate of diversification and the steady-state level of diversity. We may generate several hypotheses for these effects:

1. By intermittently redistributing and even renewing resources, disturbance may limit the intensity of divergent selection for the limiting resource. Also, by intermittently redistributing individuals across the landscape, disturbance would hinder evolutionary divergence due to the aggregation of different morphological types across a heterogeneous environment. Both these effects would act to delay the onset of divergence. The first effect would reduce divergent selection; the second would reduce the evolutionary response to divergent selection.
2. If disturbance (e.g. variable temperature) slows the rate of resource consumption, then the rate of diversification due to resource competition will also be slowed.
3. By imposing mortality, disturbance may eliminate rare species; if the rate of extinction in a disturbed environment is greater than that in an undisturbed environment, then the steady-state level of diversity will be lower in the former than the latter.
4. Disturbance may constrain the number of types that can exist at steady state by determining the frequency of certain habitats that would otherwise exist in the absence of disturbance. This is just a reformulation of the intermediate disturbance hypothesis cast at an evolutionary time scale that predicts a non-monotonic relationship between disturbance frequency and local diversity (Allmon *et al.*, 1998).

The effect of disturbance will also depend upon its temporal structure (Abugov, 1982). Different disturbance types (fire, storms, etc.) can have different magnitudes, frequencies and temporal correlation (Sornette, 2002). One general property of environmental variation of particular importance for ecological and evolutionary dynamics is its autocorrelation structure, which defines the statistical dependency of successive events in a series. In contrast to random fluctuations where successive values are statistically independent, autocorrelated fluctuations have serial dependency. This property of environmental variability has been the focus of much recent study because the fluctuations of many physical variables – both 'normal' (such as temperature and rainfall) and 'catastrophic' (climate shifts, earthquakes, hurricanes) events – are positively autocorrelated across a range of scales (Halley, 1996; Pelletier, 2002; Sornette, 2002). For example, Caswell and Cohen (1995) suggested that for a given frequency of disturbance, the temporal correlation of a series of disturbances may alter the outcome of interspecific competition, making co-existence more difficult (diversity was lower) in autocorrelated environments. Since then, several theoretical studies have demonstrated that extinction probabilities (Ripa and Lundberg, 1996; Petchey *et al.*, 1997; Pike *et al.*, 2004) and various aspects of population dynamics (Heino, 1998; Morales, 1999; Gonzalez and Holt, 2002) are sensitive to the autocorrelation structure of the environment. To our knowledge, however, this aspect of the temporal structure of disturbance has not been treated within the context of the evolution of diversity.

Our model of adaptive radiation is a rapidly growing and evolving microbial population of *Pseudomonas fluorescens* (SBW25). This bacterium shows rapid and repeatable adaptive radiation *in vitro* and is thus an ideal model system for our purposes (Rainey *et al.*, 2000). Previous work (Rainey and Travisano, 1998) has demonstrated the evolution of a phenotypic polymorphism from a monomorphic ancestor to be linked to the presence of spatial structure that develops in an unmixed liquid habitat. When polymorphic populations of *P. fluorescens* are switched to a well-mixed, unstructured habitat, the polymorphism is lost. It is thought that in the highly nutrient-rich medium rapid growth of the isomorphic population of this strictly aerobic bacterium generates strong intraspecific competition for oxygen. Competition creates divergent selection for different phenotypes adapted to different spatial locations in the habitat: planktonic versus surface- and bottom-dwelling films. In this study, we ask whether random and autocorrelated disturbance can alter the dynamics of diversification in *P. fluorescens*. We studied the effects of disturbance by abruptly homogenizing the habitat. This had the effect of redistributing individuals and the limiting resource (oxygen) without directly inducing mortality. We observed that disturbance significantly delayed diversification and that this delay was higher when disturbance was autocorrelated. Although the rate of accumulation of diversity was slower in the disturbed environments by the end of the experiment, diversity had converged to a similar steady-state level across disturbance treatments.

MATERIALS AND METHODS

Biological material

We used strain SBW25 of the Gram-negative bacterium *Pseudomonas fluorescens* (Rainey and Travisano, 1998) because it exhibits rapid and repeatable *in vitro* phenotypic (characterized by colony morphology when plated on agar) and ecological (characterized by the place colonized in the culture medium) diversification from an isomorphic population. Diversification occurs strictly in static liquid conditions and is inhibited – the culture remains isomorphic – in a shaken medium.

Three categories of morphotypes that arise over time were originally defined by Rainey and Travisano (1998): SM (Smooth Morph), the ancestral morphotype, is planktonic and occupies all parts of the culture medium; WS (Wrinkly Spreader) forms a film at the surface of the medium; FS (Fuzzy Spreader) occupies the bottom of the culture medium, where it also aggregates to form a film. However, as in previously published studies with SBW25 (e.g. Hodgson *et al.*, 2002), we identified four additional types within the WS form that show different morphological features and can be readily distinguished by independent plate readers. Our diversity counts thus included a total pool of seven morphological types.

Experimental design

We used a randomized design with destructive sampling of replicates through time. One hundred and eighty 15-ml sterile plastic tubes containing 6 ml of King's medium B (KB) (King *et al.*, 1954) were inoculated with an isomorphic (SM) population of *P. fluorescens* strain SBW25 (Rainey and Travisano, 1998) at a density of approximately 10^6 CFU · ml^{-1}. These microcosms were kept at 28°C in a temperature-controlled incubator.

Three treatments, each with five replicates, were used: (1) no disturbance, (2) autocorrelated disturbance and (3) uncorrelated disturbance (see below for description of the series). A disturbance when it occurred (the minimum inter-disturbance duration was 3 h or approximately every two generations) consisted of 2 min of orbital rotation at 25 rev · min^{-1} in an orbital culture rack (Fisher Scientific). We destructively harvested five microcosms per treatment on 12 occasions over the 7 days of the experiment. The sampling events were distributed as follows: every 8 h over the first 2 days, every 12 h over the third day, and then every 24 h for the remaining 4 days of the experiment. On each sampling occasion, all replicates were homogenized by vortex. Morphological richness and density were estimated by colony counts after dilution in KB, plating on KB agar and culture at 28°C for 48 h. For each replicate, at least two Petri dishes with 40–400 colonies were counted. To ascertain the repeatability of the results, the experiment was then repeated in full changing only the disturbance series (see below).

Generation of disturbance series

We used a first-order autoregressive model to generate time-series of environmental disturbance. A homogeneous Markov chain model of dichotomous environmental disturbance yields a variance spectrum that can be adjusted from strongly autocorrelated to uncorrelated (Caswell and Cohen, 1995). The transition between the two environmental states (disturbed or undisturbed) was governed by the following transition matrix:

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

where $0 < \lambda \leq 0.5$ and λ is the probability of a change in state; we therefore assumed a stationary environmental process. When $0 < \lambda < 0.5$ the disturbances are autocorrelated, and when $\lambda = 0.5$ the fluctuations are uncorrelated. Two replicate series of autocorrelated ($\lambda = 0.1$) and uncorrelated disturbances ($\lambda = 0.5$) were generated within MATLAB (version 5.0), one set for each experiment. Because the number of disturbances (frequency) was held constant for both disturbance types across both experiments, all other statistical properties (mean and variance), besides the pattern of correlation, were held constant (Fig. 1).

Statistical analyses

Analyses were conducted with SAS-STAT for Windows (version 8.2). The effects of treatment, time and the interaction between treatment and time on the number of morphs and on total population density (log-transformed) was assessed by analysis of variance

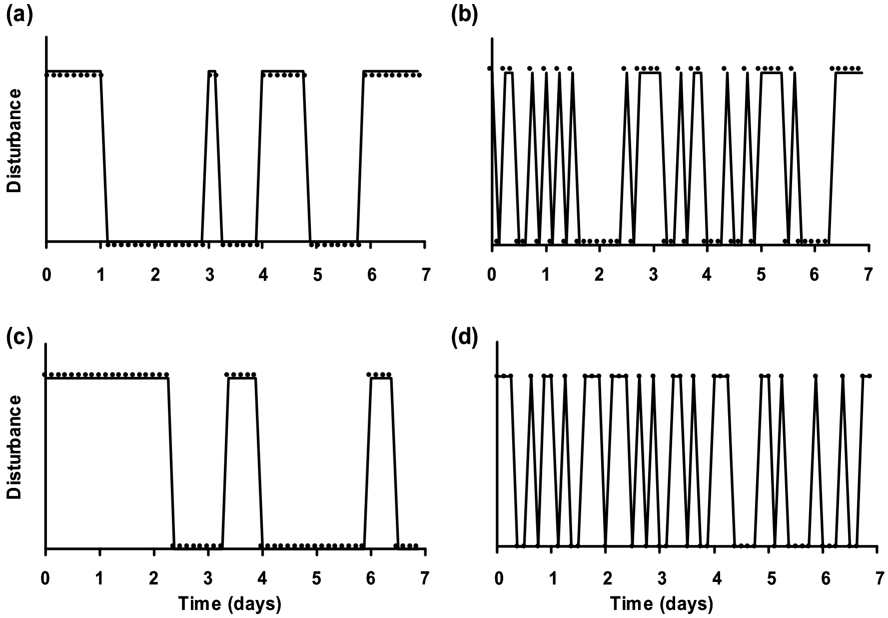

Fig. 1. Disturbance series used in the two experiments. Experiment 1: (a) autocorrelated series ($\lambda = 0.1$), (b) uncorrelated series ($\lambda = 0.5$). Experiment 2: (c) autocorrelated series ($\lambda = 0.1$) and (d) uncorrelated series ($\lambda = 0.5$).

(ANOVA). Destructive sampling at each time period ensured that each replicate was statistically independent so that repeated-measures ANOVA was not required. Divergence time was measured as the earliest time step showing an average number of morphs greater than 1, for each treatment in both experiments, and was assessed with a one-tailed *t*-test.

RESULTS

Diversity

In both experiments, there were significant effects of the disturbance treatment, time and the disturbance × time interaction on the number of morphotypes (Table 1). Interaction between time and disturbance treatment can be seen in the dynamics of morphotype richness in Fig. 2. Early in the experiment, mean morphotype richness in the disturbance treatments was lower than the undisturbed control (from a two-fold to a five-fold difference depending on experiment and time); however, this difference diminished over time as richness converged to the steady-state level in the control.

Total population density

Again differences in the dynamics of the average total population density over time resulted in significant effects of treatment, time and the treatment × time interaction in both experiments (Table 1). In Experiment 1, population density was significantly higher in the control treatment than in the two disturbance treatments at 48 h (four-fold difference) and

Table 1. Results of ANOVA on the effect of time, treatment and their interaction on mean number of morphotypes and on total population density for Experiments 1 and 2

		Time	Treatment	Time × treatment
Number of morphotypes	Exp. 1	$F_{11,180} = 68.47$ $P < 0.0001$	$F_{2,180} = 28.53$ $P < 0.0001$	$F_{22,180} = 1.97$ $P = 0.01$
	Exp. 2	$F_{11,180} = 50.74$ $P < 0.0001$	$F_{2,180} = 72.11$ $P < 0.0001$	$F_{22,180} = 3.37$ $P < 0.0001$
Total population density (ln)	Exp. 1	$F_{11,180} = 35.25$ $P < 0.0001$	$F_{2,180} = 5.04$ $P = 0.01$	$F_{22,180} = 1.73$ $P = 0.03$
	Exp. 2	$F_{11,180} = 93.01$ $P < 0.0001$	$F_{2,180} = 11.21$ $P < 0.0001$	$F_{22,180} = 3.79$ $P < 0.0001$

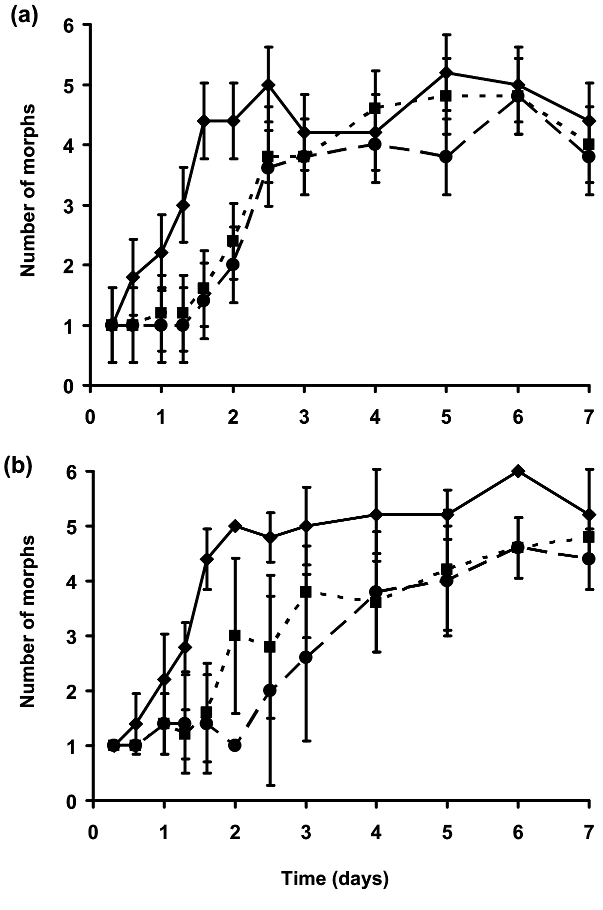

Fig. 2. Time series of the evolution of morphotype richness over the course of the two experiments: (a) Experiment 1, (b) Experiment 2. Diamonds and continuous line: control treatment; circles and broken line: autocorrelated treatment; squares and dotted line: uncorrelated series. Error bars = 1 standard deviation.

at 72 h (two-fold difference), but over the duration of the experiment the maximum difference between the means per treatment was 1.5-fold. However, in Experiment 2, it was only in the autocorrelated disturbance treatment, and at the beginning of the experiment (up to 40 h), that the total population size was significantly lower (3.5-fold difference at 32 h) than the other treatments.

Morphotype dynamics

The disturbance treatments impaired both the formation and growth of the WS and FS morphs, which appeared later and reached lower densities than in the undisturbed treatment (Fig. 3). More specifically, WS morphs were first observed 16 h on average after the experiment started in the control treatment, whereas WS morphs appeared after 24 h on average under the uncorrelated disturbance regime, and after 24 and 40 h on average in Experiment 1 and 2 respectively under the autocorrelated disturbance regime. In Experiment 2, FS never reached detectable densities (Fig. 3e) in the autocorrelated disturbance regime.

Time to divergence

Divergence was significantly delayed in both disturbance treatments in comparison to the undisturbed environment (Table 2, Fig. 2). In particular, the time to first divergence was significantly delayed by autocorrelated disturbance in both experiments, although the delay was considerably greater in the second experiment where the WS morphotype took twice as long to detect in the autocorrelated than in the uncorrelated environment.

DISCUSSION

We have shown that disturbance affects diversification during the process of adaptive radiation exemplified by *Pseudomonas fluorescens* (SBW25). In particular, disturbance resulted in longer divergence times and a slower accumulation of diversity. We also found evidence that autocorrelated disturbances may slow the rate of diversification in comparison with uncorrelated disturbances. However, as we tested only two series for each type of disturbance (autocorrelated and uncorrelated), these results should be seen as a first step towards a more complete study of the impact of disturbance correlation on evolutionary divergence.

Previous work with this model system (Rainey and Travisano, 1998) has established that phenotypic divergence is adaptive and that there is a genetic basis for diversification (Spiers *et al.*, 2002). Although the effective process underlying divergence remains unclear, evidence suggests that oxygen is the limiting resource in this nutrient-rich medium (*P. fluorescens* SBW25 is a strict aerobe) and that the existence of an oxygen gradient (a higher concentration nearer the surface that declines towards the bottom of the microcosm) in the liquid habitat is key (Rainey and Travisano, 1998). The likely reinforcement of this gradient by population growth during the course of the experiments suggests that divergence may be driven by both spatial heterogeneity and resource competition, the latter reinforcing the pre-existing oxygen gradient in the liquid habitat. This apparently simple evolutionary system therefore belies a surprisingly complex ecological interaction. By rapidly homogenizing the medium, the disturbance we imposed redistributed individuals and oxygen (resource) within the

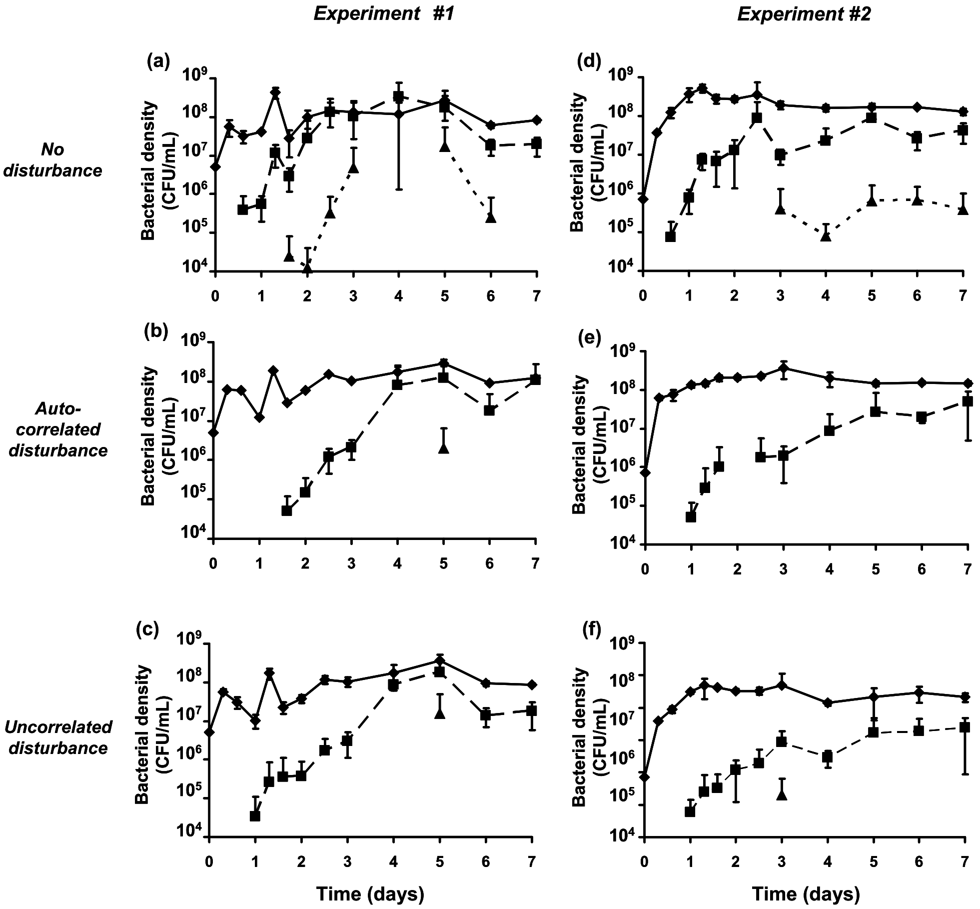

Fig. 3. Population densities for each of the three main morphotypes for each treatment over the course of the two experiments. Experiment 1: (a) control treatment, (b) autocorrelated disturbance, (c) uncorrelated disturbance. Experiment 2: (d) control treatment, (e) autocorrelated disturbance, (f) uncorrelated disturbance. Diamonds and continuous line: Smooth Morph (SM); squares and broken line: all Wrinkly Spreader morphs (WS); triangles and dotted line: Fuzzy Spreader (FS). Error bars = 1 standard deviation. The absence of a morph means either that it was not present in the population or that its concentration was too low to be detected by plating (in this case below 10^4 CFU · ml^{-1}).

habitat; an effect that destroyed the habitat structure but did not result in mass mortality, as confirmed by the small changes in population density across treatments (Fig. 3). The disturbance thus acted directly on the principal factors – resource heterogeneity and spatial aggregation – implicated in the process of ecological divergence. We suggest that the disturbance reduced divergent selection generated by competition for oxygen and by redistributing individuals throughout the habitat may have constrained the evolutionary response to this divergent selection (see hypothesis 1 in the Introduction). Previous experiments (e.g. Buckling *et al.*, 2000; Kassen *et al.*, 2004) that focused on the maintenance of diversity (in particular the intermediate disturbance hypothesis) in the same bacterial system

Table 2. Time when mean number of morphotypes was significantly greater than one (one-tailed *t*-test) for each treatment in each experiment

Experiment	Treatment	Time when mean number of morphotypes was significantly greater than one
Experiment 1	Control	0.6 day ($t_{4,5} = 4.00$; $P = 0.02$)
	Autocorrelated	2.5 days ($t_{4,5} = 10.61$; $P = 0.0004$)
	Uncorrelated	2 days ($t_{4,5} = 2.75$; $P = 0.05$)
Experiment 2	Control	1 day ($t_{4,5} = 3.21$; $P = 0.03$)
	Autocorrelated	4 days ($t_{4,5} = 5.72$; $P = 0.004$)
	Uncorrelated	2 days ($t_{4,5} = 3.16$; $P = 0.03$)

imposed disturbances of varying frequency represented by a series of mass mortality events (dilution series). In contrast, our study focused on the long-term dynamics of diversification in the absence of mass mortality that enabled us to assess the effects of disturbance correlation for a fixed frequency on divergence time.

Few theoretical studies have examined the effect of disturbance on the evolution of diversity, although several have examined the effects of temporal and spatial heterogeneity on character divergence (Schluter, 2000). For example, Day (2000) studied the impact of spatial heterogeneity on divergence and showed that features of disruptive selection depended on the movement rate between resource patches. In particular, spatial resource heterogeneity always has a disruptive effect when the migration rate between patches is low. If we consider oxygen to be the main resource that bacteria compete for, we can consider our microcosms to be spatially heterogeneous and divided into three main regions: the air–broth interface, the bottom and the rest of the culture medium. Obviously, movement within the vial was higher when disturbance (mixing) occurred than when the microcosms remained static. As we observed more evolutionary divergence in an undisturbed environment, these results qualitatively match the predictions of this model.

We also examined the effect of disturbance autocorrelation for a fixed disturbance frequency. We chose to study the effects of temporal autocorrelation on the dynamics of diversification because it has been neglected to date both theoretically and empirically. Given that disturbance events – both large and small – are autocorrelated across a range of temporal scales (Sornette, 2002), this is a surprising observation and one that may be of importance for a general theory of adaptive radiation. Although we only used two autocorrelated series and one scale of autocorrelation in these experiments, nonetheless we observed substantial and statistically significant effects on the timing of the first detectable divergence event. The only relevant study to our knowledge is that of Caswell and Cohen (1995), who explored theoretically the impact of disturbance autocorrelation on two-species competition in a metapopulation. They observed that in an autocorrelated environment, the time of recurrence of a species that was competitively excluded from a patch was greater than in an uncorrelated environment, which corroborates our findings. But clearly the structure and assumptions of Caswell and Cohen's model of competition in ecological time are not appropriate for this experimental model system and further theoretical work is required to establish the generality of their results within the context of the evolutionary dynamics of diversification.

CONCLUSION

This study addressed the fundamental question of adaptive radiation in a fluctuating environment. We have presented initial results that reveal the effects of intermittent disturbance on the dynamics of adaptive radiation. The extent to which intermittent selection is an impediment to diversification remains an open question (Schluter, 2000), but it is clear that continued neglect of this topic may constrain the generality of any theory of evolutionary diversification.

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