

REPORT

Experimental evolution of dispersal in spatiotemporally variable microcosms

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Abstract

The world is an uncertain place. Individuals' fates vary from place to place and from time to time. Natural selection in unpredictable environments should favour individuals that hedge their bets by dispersing offspring. I confirm this basic prediction using *Caenorhabditis elegans* in experimental microcosms. My results agree with evolutionary models and correlations found previously between habitat stability and individual dispersal propensity in nature. However, I also find that environmental variation that triggers conditional dispersal behaviour may not impose selection on baseline dispersal rates. These findings imply that an increased rate of disturbance in natural systems has the potential to cause an evolutionary response in the life history of impacted organisms.

Keywords

Caenorhabditis elegans, geometric mean fitness, fluctuating environments, life-history evolution, bet hedging.

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INTRODUCTION

The propensity of individuals to leave their natal habitat affects key ecological and evolutionary behaviours of the populations and the community in which they are embedded. For instance, the spread of beneficial mutations in the third phase of Wright's shifting balance is accomplished by migration among demes (Wright 1931; Wade & Goodnight 1998). Differences in dispersal rates among competing species may also alter their dominance hierarchy and, consequently, community structure (Tilman 1994). If there is heritable variation in dispersal propensity, then this life history trait is fodder for natural selection. Identifying the selective drivers of dispersal propensity may therefore provide insight into the evolution of populations and communities.

Unconditional dispersal propensity, the baseline tendency for individuals to relocate independent of their current environment, can be favoured in a stable environment as a means of reducing kin competition (Hamilton & May 1977; Motro 1983; Frank 1986; Gandon & Michalakis 1999; Perrin & Goudet 2001) or the cost of demographic stochasticity (Travis & Dytham 1998; Parvinen *et al.* 2003), but is disfavoured by variation in fitness over space (Hastings 1983; Holt 1985). A large body of literature also describes the evolution of dispersal in unstable environments, invoking either reduced competition among colonists after local disturbance (Van Valen 1971; Comins *et al.* 1980;

Olivieri *et al.* 1995; Gandon & Michalakis 1999) or reduced temporal variation (i.e. uncertainty) of geometric rates of increase (Gillespie 1977; Chesson 1981; Kuno 1981; McPeck & Holt 1992; Wiener & Tuljapurkar 1994; Holt 1997; McPeck & Kalisz 1998) as mechanisms favouring increased dispersal. I wish to address the most general prediction of this latter class of models – selection for increased dispersal propensity due to habitat instability – using simple laboratory experiments of short duration. In a separate publication (Friedenberg, unpublished data), I will extend my investigation to the effect of patch number and a metacommunity perspective.

Despite the advanced state of dispersal evolution theory, empirical evidence for a path of causation from habitat instability to dispersal propensity is lacking (Dieckmann *et al.* 1999). Field studies show that dispersal propensity is higher in variable habitats (Denno *et al.* 1996), suggesting that spatiotemporal fitness variation is at least correlated with selection on dispersal, but the complexity of natural environments and the difficulty of tracking individuals have thus far prohibited a test for causation. In this study, I attempt such a test using a bacteriophagous soil nematode, *Caenorhabditis elegans*, in artificial patchy environments. To my knowledge, my results provide the first experimental evidence that spatiotemporal environmental fluctuation is a selective driver of the evolution of dispersal propensity.

METHODS

Organism

Typically a tool for genetic and developmental studies, *C. elegans* is also an amenable system for testing haploid models of evolution. Populations can be grown in Petri plates on a non-nutritive 2.5% agar medium supplemented with a slurry of *Escherichia coli* (OP50) bacteria as food. The slurry dries on the surface of the agar to become a food patch. Individual nematodes develop and reproduce in the patches, occasionally moving between patches in the course of their life cycle. The two nematode genotypes used in this work, CB91 (Higgins & Hirsh 1977) and PD4793 (made by Kelly Liu and donated to the CGC by Donald Riddle, 1998), grow well in these conditions and can be differentiated under a properly equipped dissecting scope by the expression of a transgenic green fluorescent protein in the pharynx of PD4793. CB91 is a *rol-1* mutant; adults develop a helical twist in their cuticle that causes a right-hand bias in movement that becomes more pronounced as the adult ages. Both strains are self-fertilizing hermaphrodites, although outcrossing males are produced infrequently (Riddle *et al.* 1997). I did not observe males during the course of experiments.

Many of the mutations used to study the genetics and developmental biology of *C. elegans* affect movement behaviour (Riddle *et al.* 1997). To test for a difference in dispersal propensity between CB91 and PD4793, I placed two final-stage larvae of each genotype in one patch of a two-patch microcosm and allowed the populations to grow, reproduce and disperse for 3 days at 21 °C, enough time for a complete adult-to-adult developmental cycle. Patches were made with 70 µL of bacterial slurry and were *c.* 2 cm in diameter and 2.5 cm apart. In 20 replicate microcosms, the dispersal propensity of PD4793 exceeded that of CB91 by an average of 12.1 individuals per 100 progeny (32.3 vs. 20.2, respectively, paired SE = 3.5, d.f. = 19, $t = 3.44$, $P < 0.003$). Dispersal is surely sensitive to factors such as crowding, temperature and time, but the observed difference in dispersal propensity can be reproduced under carefully controlled conditions.

The two genotypes also differed in their fecundity over a 3-day period. I placed one final-stage virgin larva of each genotype in 48 replicate single-patch microcosms and counted the number of larval progeny after 3 days. The low dispersal genotype produced an average of 67.69 offspring, significantly higher than the high disperser's fecundity of 42.85 (paired SE = 3.72, d.f. = 47, $t = 6.67$, $P < 0.0001$). The disparity in fecundity in this short-term test can be attributed in part to later reproduction in the high dispersal genotype (Friedenberg, unpublished data). No other differences in development or foraging behaviour were observed.

Experimental design

The object of this study was to investigate the effect of spatiotemporally random environmental variation on the evolution of dispersal rate. The differential dispersal of the two worm genotypes is one of four necessary ingredients for this test. One must also be able to control the state of the environment, track changes in genotype frequency over time, and attribute those changes to environmental fluctuation rather than to within-patch dynamics or some inherent cost or benefit of dispersal in a spatially structured population.

Control of the microcosm environment is straightforward. Worms grow in patches of bacterial slurry on an agar surface. I transfer a small sample of each patch population to a corresponding patch on a fresh plate every 3 days to prevent overcrowding, starvation and contamination. Patch fitness can be manipulated by varying the number of worms that are transferred between generations. For instance, I can cause patch extinctions by failing to passage a patch population from one generation to the next, leaving an empty patch on the fresh plate. The empty patch can then be recolonized by dispersal. I can impose less severe variation by transferring large vs. small samples of worms, producing stochastic mortality.

I performed three separate experiments. The first experiment tested whether spatial structure and random extinctions influenced the evolution of dispersal. I recorded genotype frequencies every generation for five generations using two control treatments and an experimental treatment in which one randomly chosen patch went extinct every generation. The first control treatment consisted of microcosms with only a single food patch to provide baseline within-patch genotype dynamics. The second control consisted of microcosms with two patches but no variation in patch fitness. Any difference in genotype dynamics between the controls was attributable to a cost or benefit of dispersal in the absence of spatiotemporally random environmental variation. Selection for increased dispersal in a fluctuating environment was demonstrated only when the frequency of high dispersal worm was higher in treatments with two patches and random extinction than in the two-patch control. I used 10 replicate microcosms for every generation of every treatment. Patches were 70 µL of *E. coli* (OP50) slurry. All treatments began with five individuals of each genotype in one patch. I calculated frequency as the proportion of all worms in a replicate and performed an ANOVA only on the final genotype frequencies. I calculated the dispersal propensity of each genotype from their distribution after the first generation. I made an extra effort to find a single representative of a genotype in the digital images if it appeared to be extinct, thereby reducing my error associated with rarity.

The second experiment tested whether the evolution of dispersal propensity is affected by the synchrony and severity of patch fitness variation. I varied fitness by passaging a large (>100) or small (<30) number of worms each generation. In a control treatment, I varied fitness synchronously in two patches. There should be no selection on dispersal in a synchronously fluctuating environment (Cohen & Levin 1991; McPeck & Holt 1992). I used a random extinction treatment as in the first experiment to create the strongest form of selection on dispersal (Van Valen 1971). In a third treatment, I produced spatially uncorrelated, non-extinction variation in fitness. I expected the relative fitness of the high dispersal genotype in the uncorrelated variation replicates to fall between those with synchronous variation and those with random extinction (Wiener & Tuljapurkar 1994). I used 16 replicate microcosms for every generation of each treatment, initiated with five individuals of each genotype in one patch. I recorded genotype frequencies after the first and fifth generations and used the change in frequencies to calculate relative fitness according to the function $r = 1/t^* (\ln \{p/q\} - \ln \{p'/q'\})$ (Gillespie 1973), where r is the relative intrinsic growth rate of the high dispersal genotype, $t = 4$ is the number of generations between genotype counts, p is the frequency of the high dispersal genotype, q is the frequency of the high fecundity genotype and the primes signify initial conditions. I decided to present the experimental outcome in terms of realized relative fitness simply as a means of conveying information in a diverse manner and not because the data were fundamentally different from those of the first experiment. I recorded the dispersal propensity of each genotype from their distribution after the first generation.

In the third experiment, I imposed spatiotemporal variation in fitness by randomly varying the concentration of food used to create each patch. I was interested in whether intrinsic forces on fitness are as effective as extrinsically imposed calamity might be as a selective driver of dispersal propensity. All patches were made from 70 μL of bacterial slurry, but the slurry was diluted before making low-food patches. I expected low-food patches to cause low patch fitness via rapid patch depletion by adults and the subsequent starvation of offspring. For comparison with the first two experiments, I used four treatments – a single-patch control; two patches with low, synchronous variation; two patches with low, uncorrelated variation; and two patches with high, uncorrelated variation – with 13 replicates for each treatment. I produced low-severity resource fluctuations by making low-food patches with slurry diluted to half concentration. High-severity fluctuations were produced using quarter-concentration slurry for low-food patches. I recorded the frequency of

the two strains for five generations. I calculated dispersal propensities from the first generation of high- and low-variation replicates and in an additional 14 plates of each treatment.

RESULTS

In the first experiment, random patch extinctions significantly increased the frequency of the high dispersal genotype in comparison with its demise in controls with a single patch or two stable patches (Welch's ANOVA, d.f. = 2,16, $F = 9.9$, $P < 0.002$, Fig. 1). Genotype dynamics in the stable two-patch control did not differ from those in the single-patch control (Tukey HSD, $\alpha = 0.05$). The single-patch treatment, which controlled for within-patch dynamics, showed a significant decrease in the frequency of the high dispersal genotype from the first to the fifth generation (paired t -test, d.f. = 9, $t = 7.67$, $P < 0.0001$).

In the second experiment, both spatiotemporally random variation in mortality and random patch extinctions increased the relative fitness of the high dispersal genotype in comparison with its performance in synchronously fluctuating patches (d.f. = 2,45, $F = 31.58$, $P < 0.0001$). As expected, the relative fitness of the high dispersal genotype was highest with random extinction and intermediate with random variation (Tukey HSD, $\alpha = 0.05$, Fig. 2).

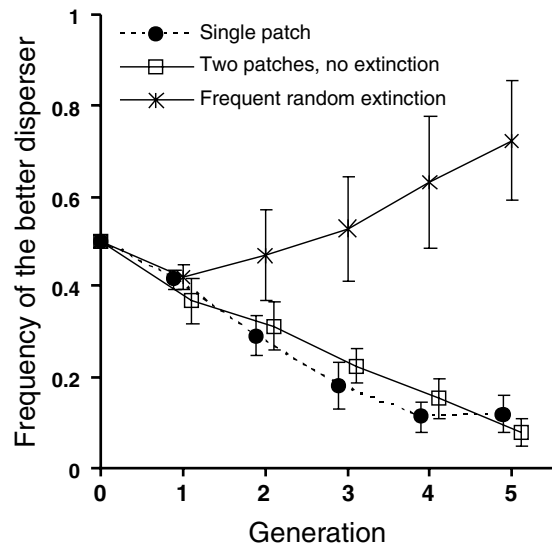


Figure 1 Change in frequency of the high dispersal genotype over five generations in three distinct spatiotemporal regimes. There was no effect of spatial structure on genotype dynamics in the absence of patch extinctions. The high dispersal genotype increased in frequency when patches were prone to random extinction. Points are treatment means of 10 replicates \pm 1 SE.

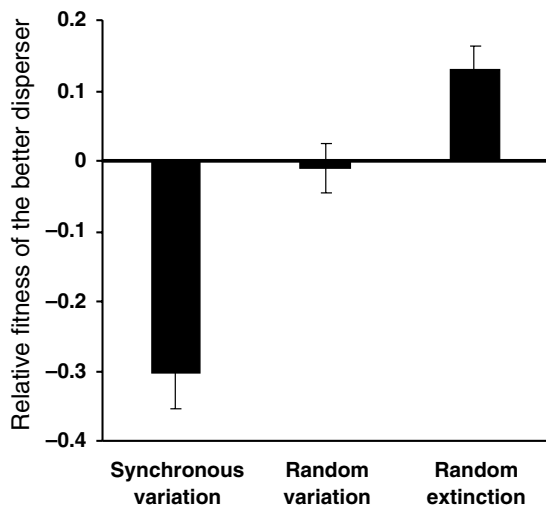


Figure 2 The effect of the synchrony and severity of patch fitness variation on the relative fitness of the high dispersal genotype after five generations. The fitness benefit of dispersal increased with the asynchrony and severity of patch fitness fluctuations. The calculation of relative fitness is described in the methods. Points are treatment means of 16 replicates \pm 1 SE.

In the third experiment, in which I varied local fitness via a manipulation of food density, neither spatial structure, asynchrony nor fluctuation severity had a significant effect on the frequency of the high dispersal genotype (d.f. = 3,48, $F = 0.49$, $P = 0.69$), although there was a trend towards higher dispersal in the high-severity treatment (Fig. 3). The high dispersal worm had a dispersal propensity of 0.18 ± 0.034 in extrinsic experiments and 0.40 ± 0.043 in the intrinsic experiment (d.f. = 133, $t = 3.94$, $P < 0.001$). The low dispersal genotype had a similar increase from 0.14 ± 0.029 to 0.36 ± 0.037 (d.f. = 133, $t = 4.6$, $P < 0.001$). Although smaller than when measured in less crowded conditions prior to the experiments, the difference between the genotypes' dispersal propensity was significant when variation was extrinsic (SE of paired difference = 0.014, d.f. = 67, $t = 2.78$, $P = 0.007$). Dispersal did not differ significantly between genotypes when variation was intrinsic (SD of paired difference = 0.033, d.f. = 66, $t = 1.10$, $P = 0.28$). There is a noticeable effect of the source of variation on the distribution of differential dispersal (Fig. 4).

DISCUSSION

As expected from both observations in nature (Gulve 1994; Roff 1994; Denno *et al.* 1996; Hill *et al.* 1999) and theoretical studies (reviewed well in Johnson & Gaines 1990; Wiener & Tuljapurkar 1994; Clobert *et al.* 2001; Mathias *et al.* 2001), spatiotemporally random environmental variation can

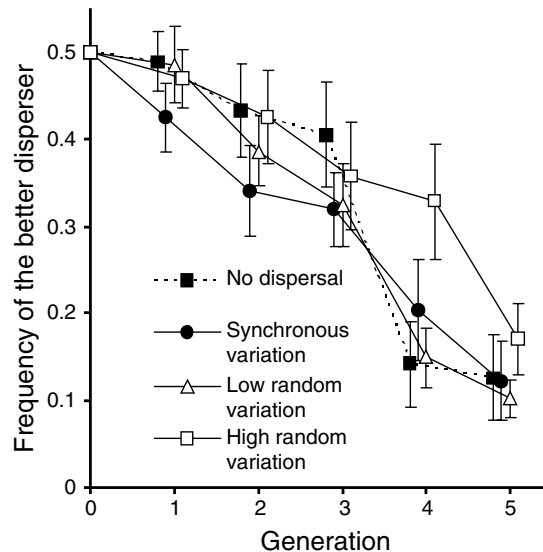


Figure 3 Change in frequency of the high dispersal genotype over five generations when fitness variation is driven by fluctuations in resource density. There was no significant effect of spatial structure or the synchrony or severity of resource fluctuations on the final genotype frequencies. Points are treatment means of 13 replicates \pm 1 SE.

favour the evolution of increased dispersal propensity. As illustrated in Fig. 1, selection strongly favoured a more fecund genotype of *C. elegans* over a genotype with higher dispersal propensity in microcosms with single food patches, nearly fixing the more fecund worm in five generations. The addition of a second food patch had no effect on this outcome, suggesting that dispersal between patches had no cost or benefit in this particular system. Dispersal is likely to be costly in nature, diminishing the ESS dispersal rate (Comins *et al.* 1980). However, the experimental microcosms were benign environments and the distance between patches was small (<2.5 cm). The more fecund genotype was also favoured in microcosms with spatially synchronous variation in mortality (Fig. 2). In contrast, spatiotemporal variation in non-extinction mortality equalized the fitness of the two genotypes (Fig. 2) and random extinctions led to an increase in the frequency of the better disperser (Figs 1 and 2).

The advantage of dispersal in a spatiotemporally variable environment may derive either purely from a reduction in the variation of short term population growth rates (*sensu* Wiener & Tuljapurkar 1994) or from the additional benefit of decreased density-dependent competition among colonists (*sensu* Gandon & Michalakis 1999). While I have not measured the relative contributions of each factor, the serial transfer of populations to fresh microcosms was intended to prevent strong density dependence within patches in the

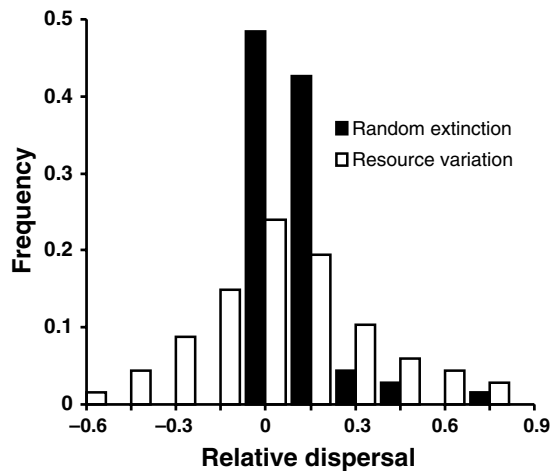


Figure 4 The frequency distribution of relative dispersal in microcosms with random patch extinction vs. resource variation. Relative dispersal is the amount by which the high dispersal genotype's dispersal exceeded that of the high fecundity genotype. Means of the distributions do not differ, but behaviour was more consistent in microcosms with random extinction.

experiments with extrinsic environmental variation. Future work in this system could explicitly address the relative roles of risk avoidance vs. colonization.

Unlike a computer simulation, experimental evolution incorporates the unmeasured biological complexity of real organisms. Although my intention was to test the evolution of unconditional dispersal and therefore to control conditions in such a manner that the differential dispersal of genotypes was consistent (i.e. to simulate unconditional dispersal), I found that the outcome of the experiments was strongly dependent upon the source of environmental variation. When I tried manipulating patch fitness intrinsically by varying resource density rather than extrinsically by varying survival, there was no significant increase in the frequency of the high dispersal genotype. Variation in resource density led to a modification in the behaviour of both genotypes, increasing and homogenizing (Fig. 4) their tendencies to move between patches. Indeed, low-resource patches were occasionally depleted and abandoned, yielding very high and homogeneous measurements of dispersal. The ability of *C. elegans* to sense and react to gradients of soluble and volatile attractants (de Bono & Bargmann 1998; Hill *et al.* 1999), that is, to forage, eroded the role of dispersal as a bet-hedging strategy at the small spatial scale of the microcosm. Whereas unconditional responses are adaptations to unpredictable changes in the environment, responses based upon information about an individual's surroundings, such as habitat-dependent (McPeck & Holt 1992; Doncaster *et al.* 1997) and density-dependent (Janosi & Scheuring 1997) dispersal, are examples of phenotypic

plasticity and evolve under a different constellation of selective pressures and scales (Levins 1963; Stearns 1976; Bradford & Roff 1993). Although evolutionary in one case and behaviourally plastic in the other, both intrinsic and extrinsic sources of environmental variation produced increases in overall dispersal rates in my experiments. Future work in this system could address the evolution of conditional dispersal using genotypes that differ in their ability to sense local cues of resource and conspecific densities.

The realized effect of habitat fluctuations on the evolution of dispersal will depend on the nexus of conditional and unconditional responses to the environment. For instance, an organism could be sensitive to fine-grained local variation, such as the density of conspecifics (Herzig 1995; Janosi & Scheuring 1997; Aars & Ims 2000), while traits related to long-distance dispersal might be determined by environmental stochasticity at a scale surpassing the organism's scope of sensation. Thus, spatial scale may distinguish the evolution of unconditional dispersal from that of, for instance, active habitat selection. However, it is important to recognize that multiple factors will impose selection on dispersal at once, sometimes acting in opposite directions (Gandon & Michalakis 2001). The degree to which dispersal rates are able to respond to selection will depend on the relative strength of such opposing forces, as well as environmental factors causing migration (Pease *et al.* 1989) and trade-offs with other fitness-related traits (Denno *et al.* 1989; Roff 1990).

A path of causation from habitat stability to selection for increased dispersal has both ecological and evolutionary consequences. Genotypic variance in behaviours or morphologies that affect dispersal propensity could play a key role in fragmented landscapes where localized disturbance is often more frequent and more severe (Pimm *et al.* 1988; Tilman *et al.* 1997). Declines in population size with increasing fragmentation can also favour dispersal (Travis & Dytham 1998; Parvinen *et al.* 2003). On the one hand, selection for increased dispersal might lead to the decline or extinction of less vagile species, as has been observed in British butterflies (Thomas 2000). On the other hand, a population can respond both behaviourally and evolutionarily to new regimes of disturbance. Via an increase in dispersal within populations, habitat instability could lead to changes in correlated traits such as reproductive effort (Ronce & Olivieri 1997; Ronce *et al.* 2000) or local adaptation (Kisdi 2002). Elevated dispersal has also been shown to encourage the evolution of pesticide resistance (Ives & Andow 2002; Carriere *et al.* 2003) and species range expansion (Gomulkiewicz *et al.* 1999; Kawecki 2000; Holt 2003). Dispersal propensity has been shown to rapidly decrease in isolated populations (Cody & Overton 1996) and in experimental populations in which disturbance was

spatially heterogeneous (Nakajima & Kurihara 1994). The growing body of theory, field observations and empirical tests concerning the evolutionary ecology of dispersal may thus not only improve our understanding of current ecological patterns but also lead towards an informed prediction of the consequences of landscape change given particular organismal or community traits.

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