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# Source Populations Act as Coevolutionary Pacemakers in Experimental Selection Mosaics Containing Hotspots and Coldspots

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ABSTRACT: Natural populations of hosts and their enemies are often spatially structured, with patches that vary in the strength of reciprocal selection, so-called coevolutionary hotspots and coldspots with strong or weak reciprocal selection, respectively. Theory predicts that dispersal from hotspots should intensify coevolution in coldspots, whereas dispersal from coldspots should weaken coevolution in hotspots; however, there have been few empirical tests. We addressed this using paired populations of the bacterium *Pseudomonas fluorescens* and the phage SBW25Φ2 linked by one-way dispersal. Within each population, the strength of reciprocal selection was manipulated by altering the bacteria-phage encounter rate, which changes the rate of coevolution without affecting environmental productivity. We observed that dispersal from hotspots accelerated coevolution in coldspots, while dispersal from coldspots decelerated coevolution in hotspots. These results confirm theoretical predictions and suggest that source populations can act as coevolutionary "pacemakers" for recipient populations, overriding local conditions.

*Keywords:* geographic mosaic theory, host-parasite, coevolution, resistance, infectivity, experimental evolution.

## Introduction

Antagonistic coevolution, the process of reciprocal selection for defense and counterdefense between hosts and their enemies, is pervasive in biological communities and thought to have a wide range of ecological and evolutionary consequences, including driving population dynamics (Thompson 1998; Loeuille et al. 2002; Yoshida et al. 2003, 2007), the evolution of diversity (Frank 1993; Benkman 1999; Schluter 2000; Buckling and Hodgson 2007), and the evolution of parasite virulence (Bull 1994; Gandon and Michalakis 2000; Gandon et al. 2002; Woolhouse et al. 2002). Coevolving populations of hosts and their enemies are often spatially structured, occurring as a set of patches connected by dispersal. The geographic mosaic theory posits that variation in ecological conditions between patches can lead to differences in local selection, generating mosaics in adaptation (Thompson 2005). This can potentially lead to variation in the strength of reciprocal selection between hosts and parasites in different patches, such that some patches display reciprocal selection (hotspots), while others do not (coldspots; Gomulkiewicz et al. 2000). Dispersal and gene flow between these patches can then act to redistribute genotypes and alleles across the selection mosaic (Thompson 1999, 2005).

A key theoretical prediction is that coevolutionary hotspots need not be ubiquitous to have an effect on the evolutionary dynamics of an interaction across the selection mosaic as a whole (Thompson 2005). Specifically, coevolutionary hotspots can drive coevolution in coldspots, provided there is gene flow and sufficiently strong selection within the hotspot (Gomulkiewicz et al. 2000). However, coldspots can also influence evolutionary dynamics in hotspots under certain conditions. For example, when hotspots are surrounded by coldspots, gene flow can lead to the swamping of the hotspot with coldspot-adapted genotypes, which can override local conditions by weakening the response to reciprocal selection pressures (Nuismer et al. 2003). Taken together, these findings lead to the theoretical prediction that dispersal from hotspot to coldspot should intensify coevolution in the coldspot, whereas dispersal from coldspot to hotspot should weaken coevolution in the hotspot.

Geographic variation in the strength of reciprocal selection has been inferred in a number of natural host-enemy systems (Benkman 1999; Kraaijeveld and Godfray 1999; Brodie et al. 2002; Thompson and Cunningham 2002; Thrall and Burdon 2003; Thompson 2005; Laine

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2006; Toju and Sota 2006; Hanifin et al. 2008). Indeed, much empirical data suggest that classification into coevolving hotspots and noncoevolving coldspots may be rather too simplistic (Nash 2008) and that there is often likely to be a continuum of intensity of reciprocal selection strength between pure coldspots and extreme hotspots (Kraaijeveld and Godfray 1999; Brodie et al. 2002; Thrall and Burdon 2003; Toju 2008). A number of ecological factors have been suggested to cause variation in reciprocal selection pressures; these include abiotic factors, such as environmental productivity (Hochberg and van Baalen 1998; Lopez-Pascua and Buckling 2008) and climate (Toju and Sota 2006; Toju 2008), and biotic factors, such as host-enemy encounter rates (Laine 2006) and the presence/absence of other interacting species (Benkman et al. 2001; Thrall et al. 2007). However, while geographic variation in reciprocal selection appears to be widespread in natural populations and its importance is highlighted by theory (Thompson 2005), there have been few explicit empirical tests of its impact on coevolutionary dynamics in selection mosaics connected by dispersal.

One reason for this lack of direct empirical data is that controlled, replicated coevolution experiments are extremely difficult to conduct in natural populations where the spatial and temporal scales are large and rates of dispersal and historical relationships between patches are difficult to determine and control. For these reasons, laboratory populations of bacteria and their viral parasites, phage, have emerged as key model systems for testing aspects of the geographic mosaic theory (Forde et al. 2004, 2007; Morgan et al. 2005, 2007; Brockhurst et al. 2007*b*; Lopez-Pascua and Buckling 2008; Vogwill et al. 2008). The bacterium *Pseudomonas fluorescens* SBW25 and its naturally associated phage SBW25Φ2 have been used extensively to test coevolutionary theory (Brockhurst et al. 2007*a*). Persistent arms race coevolution with directional selection for increased bacterial resistance and phage infectivity range has been observed, suggesting a multilocus gene-for-gene interaction (Buckling and Rainey 2002; Poullain et al. 2008). Crucially, because population samples can be cryogenically stored in "suspended animation," it is possible to directly measure rates of coevolutionary change through time. Increasing within-population mixing by periodically shaking culture vessels has been shown to increase the strength of reciprocal selection by raising the bacteria-phage encounter rate; this strengthens selection for resistance and, by extension, for novel infectivity—thereby accelerating coevolution, approximately doubling its rate—but has no affect on environmental productivity (Brockhurst et al. 2003). Here, we use this simple environmental manipulation to create patches within experimental landscapes that vary in the strength of reciprocal selection (strong reciprocal selection/with population mixing, henceforth PM$^+$; weak reciprocal selection/without population mixing, henceforth PM$^-$).

Experimental landscapes each consisted of two populations of *P. fluorescens* and SBW25Φ2 connected by unidirectional dispersal such that one population acted as a source of migrants and the other as a recipient of migrants. Four possible source-recipient arrangements were investigated: (1) PM$^-$ source–PM$^-$ recipient, (2) PM$^+$ source–PM$^+$ recipient, (3) PM$^-$ source–PM$^+$ recipient, and (4) PM$^+$ source–PM$^-$ recipient. Arrangements 1 and 2 represent homogeneous landscapes, while 3 and 4 are heterogeneous with regard to population mixing and therefore the strength of reciprocal selection. In addition, two rates of between-population dispersal were investigated. Populations were propagated by batch culture for a total of 12 transfers, and every two transfers the rate of coevolution in each recipient population was measured. We also measured the baseline rate of coevolution in isolated PM$^+$ and PM$^-$ populations that received no migrants.

## Material and Methods

### Culturing Techniques

Populations were propagated by batch culture in 30-mL glass universal bottles with loose-fitting plastic caps containing 6 mL of standard King's B medium (KB) in an incubator at 28°C. PM$^-$ populations were incubated statically; PM$^+$ populations were shaken for 1 min every 30 min at 200 rpm (Brockhurst et al. 2003). A 60-μL aliquot of each population was transferred to fresh media every 48 h. Samples of culture were stored at −80°C in 20% glycerol. Phage populations were isolated by centrifuging samples of culture in 10% chloroform (which lysed and pelleted bacterial debris) and then stored at 4°C.

### Experimental Design

Forty-eight replicate populations (24 PM$^-$ populations and 24 PM$^+$ populations) were founded with $10^5$ clonal particles of phage and $10^7$ *Pseudomonas fluorescens* SBW25 cells and allowed to coevolve for six transfers before beginning dispersal treatments. After this period, populations were assigned into source-recipient pairs to create six replicates of each of the following source-recipient arrangements: (1) PM$^-$ source–PM$^-$ recipient, (2) PM$^+$ source–PM$^+$ recipient, (3) PM$^-$ source–PM$^+$ recipient, and (4) PM$^+$ source–PM$^-$ recipient. Each source-recipient pair was used to found two experimental landscapes, one to undergo 1% dispersal and one to undergo 10% dispersal. Six PM$^+$ and six PM$^-$ recipient populations were also used to found isolated populations that received no migrants. We transferred 60-μL aliquots to fresh microcosms every

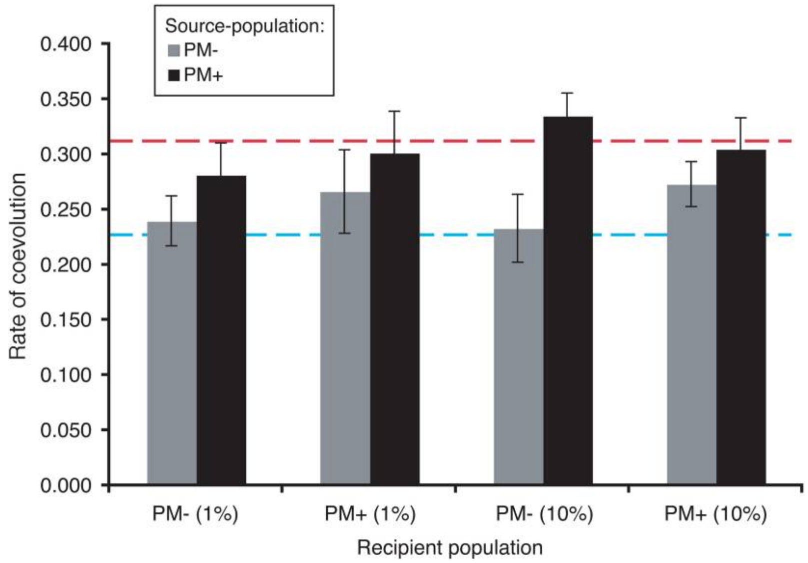

**Figure 1:** Rate of coevolution in recipient populations. Bars represent the mean rate of coevolution averaged through time ± SE in recipient populations. Dashed lines represent the mean rate of coevolution in isolated PM$^+$ (*red*) and PM$^-$ (*blue*) populations that received no migrants. Source population refers to the population-mixing regime in the source population, while recipient population refers to the population-mixing regime in the recipient population. Rates of between-patch dispersal are provided in parentheses.

48 h for a total of 12 transfers. Source to recipient population dispersal was achieved by, for each recipient population, a defined portion of this transferred aliquot being contributed by the corresponding source population. Depending on the dispersal rate, this involved transferring either 54 $\mu$L of recipient population and 6 $\mu$L of source population to a fresh microcosm (10% dispersal rate) or 59.4 $\mu$L of recipient population and 0.6 $\mu$L of source population (1% dispersal rate).

### *Measuring Coevolution*

Bacterial resistance for a given population was determined by isolating 10 bacterial colonies on KB agar, which were then streaked across a perpendicular line of phage that had been previously dried onto a KB agar plate. Any bacterial colonies that showed growth inhibition on encountering the line of phage were classed as sensitive. Resistance was measured as the proportion of resistant bacterial colonies. Antagonistic coevolution between *P. fluorescens* and SBW25Φ2 has been shown to be predominantly escalatory with directional selection for increasing infectivity and resistance through time (Buckling and Rainey 2002; Brockhurst et al. 2003). To determine the rate of coevolution, we measured how the infectivity of phage populations to a bacterial population changed through time. Specifically, every two transfers, we determined the resistance of bacterial populations to past (two transfers previous) and future (two transfers subsequent) phage populations from the same replicate line. If directional coevolution was occurring, then we would expect, for multiple time points, future phage to be better than past phage at infecting contemporary bacteria, hence a positive slope of infectivity against time: the magnitude of this slope gives a measure of the rate of coevolutionary change (Brockhurst et al. 2003, 2007*b*; Lopez-Pascua and Buckling 2008; Vogwill et al. 2008).

### *Statistical Analysis*

Rates of coevolution were averaged through time and analyzed using a linear mixed model performed in SPSS. Source population mixing, recipient population mixing, and dispersal rate were fitted as fixed factors, while founding population was fitted as a random factor nested within both source and recipient population mixing.

## Results

In the absence of immigration, population mixing had a significant effect on the strength of reciprocal selection within populations ($F_{1,10} = 12.62$, $P < .01$), confirming that the PM$^+$ treatment created hotspots (mean rate of coevolution = 0.312 ± 0.016) while the PM$^-$ treatment created coldspots (mean rate of coevolution = 0.226 ± 0.018). Within experimental landscapes, the coevolution-

**Table 1:** Test of fixed effects

| Source | Numerator df | Denominator df | *F* | *P* |
|---|---|---|---|---|
| Intercept | 1 | 20 | 510.825 | <.001 |
| SPM | 1 | 20 | 4.503 | .047 |
| RPM | 1 | 20 | .328 | .573 |
| DR | 1 | 20 | .840 | .370 |
| SPM × RPM | 1 | 20 | .600 | .448 |
| SPM × DR | 1 | 20 | .840 | .370 |
| RPM × DR | 1 | 20 | .352 | .560 |
| SPM × RPM × DR | 1 | 20 | 1.049 | .318 |

Note: SPM = source population mixing; RPM = recipient population mixing; DR = dispersal rate.

ary rate of recipient populations was determined by population mixing in the source population (fig. 1; $F_{1,20} = 4.503$, $P = .047$) but not by population mixing in the recipient population itself (fig. 1; $F_{1,20} = 0.328$, $P = .573$) or by the rate of immigration (fig. 1; $F_{1,20} = 0.840$, $P = .370$), and there were no significant interactions between main effects (table 1). Therefore, as predicted, immigration from $PM^+$ source populations increased the rate of coevolution in $PM^-$ recipient populations, while immigration from $PM^-$ source populations decreased the rate of coevolution in $PM^+$ recipient populations, relative to equivalent recipient populations in homogeneous landscapes.

## Discussion

Central to the geographic mosaic theory is the concept of selection mosaics with patches that vary in intensity of reciprocal selection, so-called coevolutionary hotspots and coldspots (Thompson 2005). Such geographic variation in reciprocal selection intensity appears to be widespread in natural host-enemy populations (Benkman 1999; Kraaijeveld and Godfray 1999; Brodie et al. 2002; Thompson and Cunningham 2002; Thrall and Burdon 2003; Laine 2006; Toju and Sota 2006). In this study, we experimentally manipulated the strength of reciprocal selection within populations through altering host-parasite encounter rates without affecting environmental productivity. Our results suggest that heterogeneity in the strength of reciprocal selection across a landscape is an important determinant of coevolutionary dynamics within population patches. Specifically, for recipient populations in heterogeneous landscapes, immigration from a patch with stronger reciprocal selection can accelerate coevolution, while immigration from a patch with weaker reciprocal selection can decelerate coevolution. This suggests that source populations can act as coevolutionary "pacemakers" for recipient populations, overriding local conditions.

It is notable that only low to moderate rates of dispersal were required to override local selection: as little as 1% immigration every ~7.5 host generations. It is somewhat surprising, however, that there was no significant effect of different rates of dispersal on coevolution in our experiment. Specifically, theory predicts that coevolutionary dynamics in coldspots should be more likely to resemble those in hotspots as the migration rate increases from low to moderate levels (Gomulkiewicz et al. 2000). It is possible that the two rates of dispersal (1% and 10%) used in our experiment were too similar to detect a significant difference, both being in effect moderate rates of dispersal, and that an even lower dispersal rate would be required to detect the pattern predicted by theory. It is interesting to note that another recent study on the effects of dispersal rate on adaptation also found little difference between the effects of 1% and 10% dispersal (Venail et al. 2008).

Hosts and parasites were codispersed at equal rates in our experiment. While in some host-parasite associations such congruent patterns of host and parasite gene flow are observed (Mulvey et al. 1991), in certain others, patterns of host and parasite gene flow are decoupled, with either the host (Delmotte et al. 1999) or the parasite (Dybdahl and Lively 1996; Davies et al. 1999) displaying relatively greater levels of gene flow. As in previous studies (Forde et al. 2004, 2007; Morgan et al. 2007), our findings may therefore be somewhat limited to host-parasite systems that experience simultaneous host-parasite dispersal. Such situations are likely to arise where the parasite is reliant on the host for its dispersal, as is the case for contact-transmitted parasites, or where codispersal of host and parasite is driven by an external factor such as a prevailing wind or an aquatic current.

These results confirm, along with the findings of a previous experimental study that manipulated environmental productivity (Forde et al. 2007), that dispersal from hotspots can "warm up" coevolution in coldspots. However, ours is the first, as far as we are aware, to show empirically that dispersal from populations with weaker reciprocal selection can "cool down" those with more intense reciprocal selection. This has been shown to be theoretically possible (Hochberg and van Baalen 1998; Gomulkiewicz et al. 2000; Nuismer et al. 2003; Thompson 2005); however, it is important to consider whether hotspots or coldspots are likely to predominate in natural selection mosaics. In selection mosaics generated by productivity gradients, where there is likely to be a positive relationship between productivity and population density (Lopez-Pascua and Buckling 2008), it is probable that hotspots will have a greater impact because they will act as net sources of migrants, while coldspots will act as net recipients. However, where reciprocal selection is weakened through reduced host-parasite encounter rate (Laine 2006), such coldspot populations may act as net sources of migrants as a result of lower incidence of parasitism, which can negatively regulate host population growth in nature (Tompkins et al. 2002). In addition, geographical limitations to dispersal may often result in unidirectional movement of migrants (e.g., aquatic currents, prevailing winds); under such conditions, coldspots or hotspots that act as net sources of migrants are likely to determine coevolutionary dynamics across the selection mosaic.

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