Gene Flow Reverses an Adaptive Cline in a Coevolving Host-Parasitoid Interaction

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abstract: Many natural populations are characterized by clinal patterns of adaptation, but it is unclear how gene flow and environmental gradients interact to drive such clines. We addressed this question by directly manipulating dispersal and productivity in an experimental landscape containing a microbial parasitoid, the bacteriophage T7, and its host, the bacterium *Escherichia coli*. We observed that the adaptation of parasitoids increased on hosts originating from lower-productivity communities in the absence of gene flow. However, adaptation decreased along the same productivity gradient with experimentally imposed gene flow of the host and parasitoid. This occurred despite relatively low rates of gene flow.

Keywords: adaptation, bacteriophage, coevolution, *Escherichia coli*, environmental gradient, gene flow.

Species often coevolve across complex landscapes, creating locally coadapated populations that are connected by gene flow. This geographic mosaic of coevolution (Thompson 1994, 2005) can create patterns in adaptation ranging from clearly defined mosaics to smooth clines (Kraaijeveld and Godfray 1999; Benkman et al. 2001; Brodie et al. 2002; Thrall et al. 2002; Johnson and Herbers 2006; Laine 2006; Toju and Sota 2006). Well-defined coevolutionary mosaics are often readily interpretable, resulting from discrete differences among ecosystems in physical environments or from the presence or absence of other species. Clinal variation in coevolving species, however, is more difficult to interpret because it may result directly from local coadaptation across a physical or biotic gradient, secondary contact, or gene flow between genetically distinct populations across homogeneous environments. Here we show experimentally that clines in adaptation of parasitoids to their hosts can switch direction depending on the opposing forces of gene flow and environmental gradients.

How gene flow shapes adaptation across environmental gradients has been a long-standing question in evolutionary biology (Slatkin 1973; Endler 1977) and has become increasingly important in coevolutionary studies in natural populations, managed populations, and epidemiology (Colizza et al. 2006). Organisms are faced with environmental gradients generated by differences in abiotic and biotic factors, such as temperature, salinity, agricultural runoff, and invasive species (Brönmark and Hansson 2002; Pimental 2002; Thompson et al. 2002*b*). In addition, rapid transport of parasites has become commonplace in our mobile societies (Pimental 2002), thereby creating complex patterns of gene flow among populations. Evolutionary studies have suggested that large-scale clines in adaptive traits for some coevolving parasites and hosts are due to coadaptation across abiotic and biotic gradients and/or migration (Kraaijeveld and Godfray 1999; Toju and Sota 2006). Moreover, research on rapidly coevolving species has shown that low levels of gene flow can increase local adaptation in host-parasite interactions (Forde et al. 2004; Morgan et al. 2005). Observed clines of adaptation in interacting species have shown patterns ranging from strong to weak adaptation with increasing geographic distance (Ebert 1994; Kaltz et al. 1999), and mathematical models of coevolution have suggested that gene flow and environmental gradients together can produce complex clines in coevolving species (Hochberg and van Baalen 1998; Case and Taper 2000; Nuismer et al. 2000; Kawecki and Holt 2002; Lett et al. 2005). Nevertheless, no experimental work to date has explicitly evaluated the relative importance of gene flow and abiotic gradients in generating patterns of adaptation across space in coevolving species.

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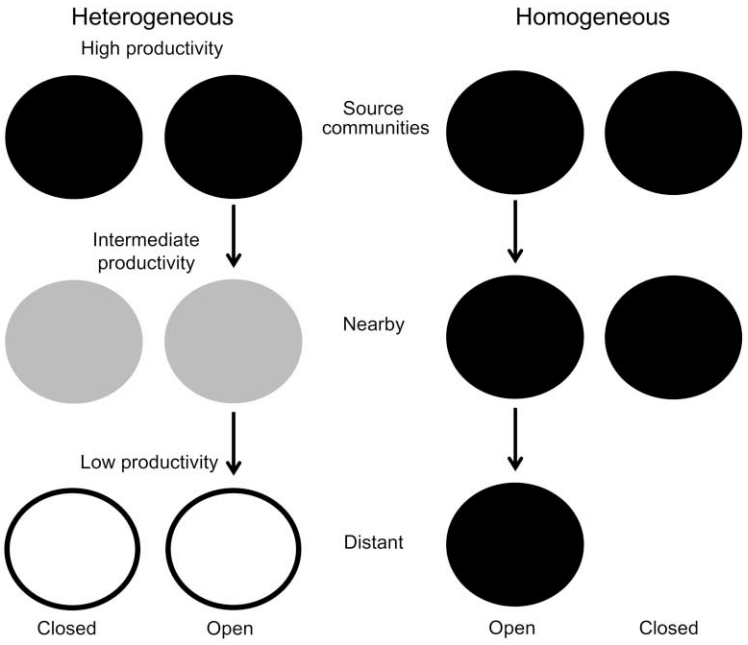

Figure 1: Experimental landscapes. Circles represent communities with different levels of productivity that are either open or closed to dispersal. Circle color indicates the productivity level: *black* = high, *gray* = intermediate, *white* = low. Open communities (with arrows between them) are designated as either near or far from the source community. Note that there are only two communities in the homogeneous closed landscape because "near" and "far" are irrelevant when there is no dispersal. In the closed heterogeneous landscape, the third community serves as a control for the open low-productivity community.

We experimentally evaluated how gene flow and an environmental gradient could interact to shape clinal patterns of adaptation of a parasitoid to its host over hundreds of generations. We manipulated gene flow of the parasitoid and host across productivity (i.e., nutrient) gradients in experimental microcosms of a parasitoid (bacteriophage T7) and its host (bacterium *Escherichia coli*). Bacteria and bacteriophage have proven particularly useful for studies of antagonistic coevolution (Chao et al. 1977; Lenski and Levin 1985; Shrag and Mittler 1996; Buckling and Rainey 2002; Mizoguchi et al. 2003; Morgan et al. 2005). Unlike most field systems, laboratory experiments with microbes allow for direct control over dispersal and the environment in which the organisms interact. In many field systems, environmental gradients are multivariate—for example, latitudinal gradients can be driven by correlations among productivity, temperature, and/or light levels. In contrast, in our study system we can directly manipulate the productivity gradient. Further, changes in host resistance and parasitoid effectiveness can be followed over hundreds of generations.

The coevolutionary dynamics of *E. coli* and T7 can be divided into a series of phenotypic classes based on patterns of resistance and counterresistance (Chao et al. 1977). Ancestral T7-sensitive bacteria (B_0) evolve resistance to ancestral phage ($T7_0$), after which they are referred to as first-order resistant bacteria (B_1). The T7 can then evolve to attack the first-order resistant bacteria and are referred to as host-range mutants ($T7_1$), which can also attack B_0. Second-order resistant bacteria (B_2) that are resistant to $T7_0$ and $T7_1$ can also arise and eventually invade the community.

We tested whether dispersal of the T7 and its host *E. coli* along an environmental gradient resulted in clines in the adaptation of T7 by establishing four stepping-stone experimental landscapes of microbial communities (fig. 1). At the start of the experiment, continuous-culture devices (chemostats) were inoculated with isogenic strains of *E. coli* and T7. This allowed us to directly follow the processes underlying patterns in adaptation in the coevolving pair, whereas in many study systems, processes can only be inferred. Productivity levels determine the generation times and/or population sizes of bacteria and bacteriophage (Bohannan and Lenski 1997, 2000), which should ultimately influence adaptation of T7 to its host. Increasing productivity increases the population sizes of $T7_0$ and B_1, on average (fig. 2; Bohannan and Lenski 1997), and decreases the generation times of B_0 (Bohannan and Lenski 1997). Further, low-productivity environments can slow or prevent the evolution of B_1 and B_2 (Bohannan and

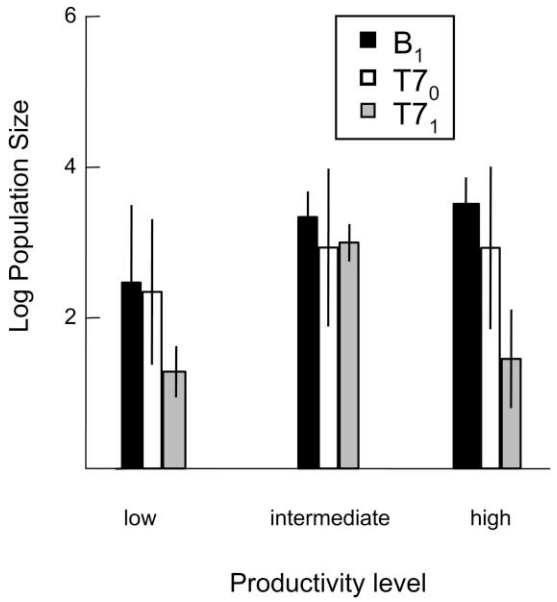

Figure 2: Population sizes of $T7_0$, $T7_1$, and B_1 averaged for days 9 and 13 ($\pm$SE) from the closed heterogeneous landscape.

Lenski 2000), which should also shape patterns of coevolution. The degree of resistance or virulence in antagonistic interactions can vary with environmental gradients and can underlie adaptive clines (Hochberg and van Baalen 1998; Kraaijeveld and Godfray 1999; Hochberg et al. 2000).

We predicted that T7 from the high-productivity source communities should have higher fitness on B_1 from low-productivity communities than on B_1 from the intermediate-productivity communities because high-productivity bacteriophage should be ahead of lower-productivity bacteria in the coevolutionary arms race. In contrast, theory predicts a decreasing relationship between adaptation and geographic distance (Ebert 1994) that results in a decrease in bacteriophage fitness with dispersal distance (i.e., hosts from the same, nearby, and distant patches). Thus, the forces of the environmental gradient and gene flow on patterns of adaptation should oppose one another.

We were then able to distinguish between the effects of gene flow and the productivity gradient on clines in bacteriophage adaptation in two ways. First, the homogeneous landscape, where productivity levels remained constant across space, allowed us to assess the pure effects of gene flow with distance on bacteriophage infectivity. Second, a series of assays of adaptation of the bacteriophage from the low-productivity communities on hosts from higher-productivity communities in the heterogeneous landscape allowed us to verify our conclusions that gene flow reversed the adaptative cline initially driven by the productivity gradient.

Material and Methods

Study System

At the start of each run of the experiment, all chemostats were inoculated with the same ancestral strains of T7 bacteriophage (obtained from the American Type Culture Collection) and of *Escherichia coli* B (strain REL 607; Bohannan and Lenski 1997). Evolution of $T7_1$ from $T7_0$ most often occurs through mutations that change the T7 tail fibers, resulting in an expanded host range (i.e., $T7_1$ are able to attack both sensitive and resistant bacteria). Because T7 directly kills the bacteria that it infects and because the generation time of T7 is shorter than that of its host, T7 can be thought of as a parasitoid rather than a parasite or predator (Godfray 1994). The change between phenotypic classes of bacteria (i.e., B_0 to B_1) most often occurs through mutations that change or eliminate the cell surface receptor molecule (Chao et al. 1977). There is usually a trade-off between resistance and competitive ability such that phage-resistant bacteria are inferior competitors for nutrients (Bohannan and Lenski 1997, 2000).

Experimental Design

The experiment was conducted in continuous-culture devices known as chemostats (Bohannan and Lenski 1997). We directly manipulated productivity levels in the communities (heterogeneous and homogeneous gradients) and dispersal of T7 and *E. coli* (open and closed treatments), resulting in four types of landscapes (fig. 1). In the heterogeneous landscapes, three levels of productivity were used (high = 1,000 μg/mL, intermediate = 100 μg/mL, and low = 10 μg/mL glucose input). Dispersal of the bacteriophage and bacteria occurred from the high-productivity community to the intermediate community to the low-productivity community. This experimental design is analogous to emigration from productive source populations, a situation common in many ecological systems (Kawecki and Holt 2002). In the homogeneous landscape, all chemostats received 1,000 μg/mL of glucose. Dispersal occurred in the same stepping-stone fashion in the open homogeneous landscape as in the open heterogeneous landscape. Chemostats that were closed to dispersal were also established in both heterogeneous and homogeneous landscapes, for a total of four different treatments (open/heterogeneous, closed/heterogeneous, open/homogeneous, closed/homogeneous). Each type of landscape was replicated three times; however, one replicate of the closed, high-productivity treatment (heterogeneous landscape) was lost to contamination. The design was therefore similar to that used in an earlier experiment (Forde et al. 2004) but differed in two important ways. First, the homogeneous landscape, where

productivity levels remained constant across space, allowed us to assess the pure effects of gene flow with distance on bacteriophage infectivity. Second, assays of adaptation of T7 to its host in the experiments described here were designed to allow us to distinguish between the relative effects of the productivity gradient and gene flow on clines in infectivity (see "Adaptation Assays").

Chemostats were sampled every 48 h. Five mL were removed from each chemostat, and 3 mL of that were used for dispersal in the open communities (10% of the community). This dispersal rate (10% of the populations every 48 h) resulted in a fraction of immigrants ranging between 0.002 and 0.005 per generation for the bacteria and the bacteriophage (Slatkin's [1985] metric "m"). The bacteria and bacteriophage were dispersed together, as is the case with endoparasites and/or parasites that cannot survive independently from their hosts. Although dispersal alters local population sizes, these changes are short-lived relative to the generation times of the bacteriophage and bacteria. There are about 105 bacteriophage generations and 21 bacterial generations in 48 h.

Another portion of the sample was used to determine population sizes of the bacteriophage and bacteria. To determine the bacteriophage population sizes, we added 30 μL of chloroform to 1,000 μL of the sample and vortexed the mixture to kill any bacteria that were present. One hundred μL of this sample was plated on a lawn of the ancestral bacteria that had been grown up over 24 h to determine the "efficiency of plating" (EOP; the number of plaques on each host), a measure of infectivity. We plated 50 μL of the original sample taken from the chemostat with 50 μL of the ancestral strain of T7 on minimal glucose agar plates to determine the population sizes of B_1. We then plated 100 μL of the original sample on minimal glucose agar plates without T7 and subtracted the number of B_1 colonies from the same chemostat to determine the population size of B_0. The remainder of the sample was stored at −80°C, which allowed for a detailed post hoc evaluation of patterns of adaptation.

Adaptation Assays

Because of the predictability in phenotypic changes in the early stages of the arms race between the bacteria and the bacteriophage, we used infectivity of the bacteriophage as an indicator of ongoing coevolution in the bacteria and bacteriophage populations (Chao et al. 1977; Forde et al. 2004). Two or three independent colonies of B_1 were isolated from the same samples from which the bacteriophage were isolated (days 9 and 13; about 475 and 675 bacteriophage generations, respectively). Using B_1 in the assays allowed us to assess counteradaptation of the bacteriophage to evolution in the hosts. For each adaptation assay, overnight cultures of the colonies were grown in 1,000 μg/mL glucose media. We plated replicate samples of T7 from the source community on a lawn of the appropriate B_1 grown from the overnight culture. For the heterogeneous treatment, we plated bacteriophage from the high-productivity community on B_1 from the high-productivity community (within), on B_1 from the intermediate community (nearby), and on B_1 from the low-productivity community (distant). This was done for the open and closed communities. Thus, increasing dispersal distance was correlated with decreasing productivity in the heterogeneous, but not the homogeneous, landscapes.

We further tested for the effect of the productivity gradient on bacteriophage adaptation by isolating T7 from the low-productivity communities and plating them on hosts from low-, intermediate-, and high-productivity communities (within, nearby, and distant patches, respectively). Finally, the same protocol was used for assays of phage adaptation in the homogeneous landscape, but the phage assays were simply plated on hosts from within, nearby, and distant patches. We used EOP on evolved hosts (B_1) as a measure of bacteriophage infectivity. EOP integrates a number of traits that can change as bacteriophage coevolve with their hosts (e.g., changes in adsorption or burst size).

Data Analysis

Data on bacteriophage infectivity described above were averaged across the two or three colonies used in the assays, resulting in a mean measure of infectivity for the bacteriophage from each replicate chemostat. Data from days 9 and 13 were averaged and log transformed to achieve normality. We were first interested in whether lin-

Table 1: Results from analyses of bacteriophage infectivity from the heterogeneous landscape

	df	*F*	*P*
A. Effect:			
Distance/productivity	2	1.263	.321
Gene flow (yes/no)	1	10.218	.009
Distance/productivity × gene flow	2	4.87	.031
Error	11		
B. Contrast (open vs. closed):			
High productivity/within patch	1	.456	.513
Intermediate productivity/nearby patch	1	7.52	.019
Low productivity/distant patch	1	14.253	.003
Error (for each contrast)	11		

Note: A = results from the two-way ANOVA; B = results from post hoc contrasts of bacteriophage infectivity from the open and closed communities for each productivity level/patch type.

ear trends across the productivity gradient in the heterogeneous landscapes differed in the open and closed communities. We analyzed the data on bacteriophage infectivity using a two-way ANOVA with dispersal (open or closed) and distance/productivity as the main effects. We then did a series of contrasts of infectivity between the open and closed communities at each distance (within, nearby, and distant patches) to evaluate the effect of gene flow on bacteriophage adaptation.

Since we were more interested in a linear trend in the means with dispersal distance than whether there were specific differences between the group means, we then tested for clinal patterns in adaptation with dispersal distance and along the productivity gradient using linear contrasts for the open and closed communities separately (Quinn and Keough 2002).

Results

We found complex clinal patterns of adaptation in the heterogeneous landscapes that depended on whether gene flow was present (table 1; fig. 3*a*). Bacteriophage adaptation was significantly different in the open and closed communities (table 1). As predicted, there was no difference in bacteriophage infectivity on within-patch hosts in the presence or absence of gene flow. However, there was a 63% decrease in infectivity on hosts from nearby patches and an 81% decrease in infectivity on hosts from distant patches in open communities compared with the same in closed communities (fig. 3*a*). Thus, the productivity gradient and gene flow had opposite effects on bacteriophage adaptation, and these differences increased with increasing distance from the source communities.

We further tested for clines in bacteriophage adaptation using a series of linear contrasts on infectivity data from the open and closed communities. There was a significant linear increase in bacteriophage infectivity with decreasing host productivity in the absence of dispersal (fig. 3*a*; high vs. low productivity: $F = 31.68$, df $= 1, 5$, $P = .002$; high vs. intermediate productivity: $F = 16.31$, df $= 1, 5$, $P = .01$). However, the direction of the cline was reversed in the presence of gene flow, which was driven by differences in infectivity between the high- (within) and low-productivity (distant) communities (fig. 3*a*; $F = 6.39$, df $= 1, 6$, $P = .045$; high/within productivity vs. intermediate/nearby productivity: $F = 3.992$, df $= 1, 6$, $P = .09$). As we predicted, the productivity gradient drove the cline in the closed communities. However, it appeared that gene flow overpowered the effect of the environmental gradient in generating the clinal patterns of adaptation in the open communities.

Assays of adaptation of T7 from the low-productivity communities on hosts from the intermediate- and high-

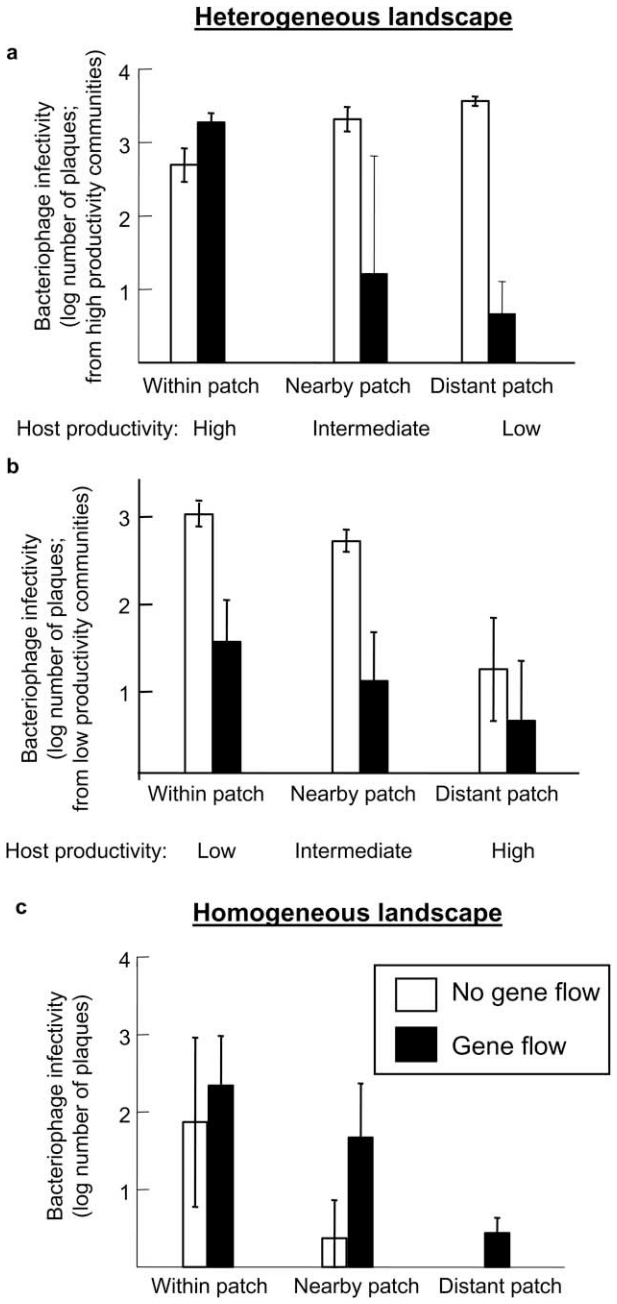

Figure 3: Adaptation (infectivity) of bacteriophages to their hosts, measured as the number of plaques per host (log transformed). Data are averaged for days 9 and 13 ($\pm$SE). *a*, Heterogeneous landscapes: infectivity of bacteriophage from the high-productivity communities on hosts from the same patch/high-productivity, nearby patch/intermediate-productivity, and distant patch/low-productivity hosts, with and without gene flow. *b*, Heterogeneous landscapes: infectivity of bacteriophage from the low-productivity communities on hosts from the same patch/low-productivity, nearby patch/intermediate-productivity, and distant patch/high-productivity hosts, with and without gene flow. *c*, Homogeneous landscapes: infectivity of bacteriophage on hosts from the same patch, nearby patch, and distant patch (open communities only) hosts, with and without gene flow.

productivity communities verified that the patterns of bacteriophage adaptation from the closed heterogeneous landscape were driven by the environmental gradient. We expected to find a decrease in bacteriophage infectivity with increasing host productivity because, in this case, phage should be behind their hosts in the coevolutionary arms race. Regardless of whether the communities were open or closed to dispersal, there was a decreasing relationship between infectivity and productivity that was statistically significant in the absence of gene flow (fig. 3*b*; $F = 15.253$, df $= 1, 6$, $P = .001$).

Assays of adaptation of T7 to *E. coli* from the homogeneous landscape further supported our conclusions. We reasoned that if productivity was in fact driving the increase in adaptation of high-productivity bacteriophage in the closed heterogeneous landscape, we should not see an increase in bacteriophage infectivity on allopatric hosts in the closed homogeneous landscape. In the absence of gene flow and the environmental gradient, bacteriophage infectivity was more than five times as great on within-patch hosts than on hosts from nearby patches (fig. 3*c*; $F = 2.732$, df $= 1, 4$, $P = .174$).

Finally, if dispersal distance was driving the decreasing cline in bacteriophage infectivity in the open heterogeneous communities, there should be a decreasing relationship between bacteriophage infectivity and distance in the open homogeneous landscape, and this is what we found (fig. 3*c*; $F = 10.26$, df $= 1, 6$, $P = .019$). This difference was driven by differences in infectivity on hosts from within the same patch as the bacteriophage versus on hosts from distant patches (within vs. nearby; $F = 1.279$, df $= 1, 6$, $P = .3$).

Discussion

Our results demonstrate that the direction of an adaptive cline generated by an environmental gradient can be reversed in the presence of gene flow. Through direct manipulations of dispersal and productivity, we were able to evaluate both the independent and joint effects of these factors on spatial patterns of adaptation for a coevolving species pair. We found that in the absence of gene flow, adaptation of bacteriophage T7 increased on hosts originating from lower-productivity environments because the parasitoids were ahead of their hosts in the coevolutionary arms race. Population sizes of both the bacteriophage and the bacteria were greater on average in the highly productive source communities than in communities characterized by lower levels of productivity, a result consistent with research in similar systems (Bohannan and Lenski 1997). Host range (T7) and bacteriophage-resistant *E. coli* mutants are more likely to arise in larger populations, thereby increasing the rate at which the coevolutionary "wheel" turns relative to smaller populations (Bohannan and Lenski 1997). However, the direction of the adaptive cline was reversed in the presence of gene flow. Adaptation of T7 decreased on hosts from more distant communities, relative to sympatric hosts, a result that is in line with theory and past research (Ebert 1994; Kaltz et al. 1999).

Our experimental design allowed us to decompose the influences of gene flow and the productivity gradient in generating the adaptive clines across the heterogeneous landscapes. In addition to evaluating adaptation of T7 from high-productivity communities on hosts from lower-productivity communities, we assayed adaptation of T7 from the low-productivity communities on hosts from the intermediate- and high-productivity communities. This analysis verified that the patterns of bacteriophage adaptation from the closed heterogeneous landscape were driven by the environmental gradient. We found a decrease in bacteriophage infectivity with increasing host productivity because, in this case, bacteriophage were behind their hosts in the coevolutionary arms race. This result supports our conclusion that the increasing cline in bacteriophage infectivity from the closed heterogeneous landscape was driven by the productivity gradient. More importantly, it strengthens our argument that the decreasing cline in adaptation in the open communities must be the result of gene flow (i.e., dispersal distance) having a stronger effect on bacteriophage infectivity than productivity.

The homogeneous landscape allowed us to look at the pure effects of gene flow on adaptation, and by comparing the results of the assays with those from the heterogeneous landscape, we were able to directly distinguish between the influence of the productivity gradient and dispersal distance on clinal patterns of adaptation. Our results supported our hypotheses once again. We hypothesized that if productivity was driving the increase in adaptation of high-productivity bacteriophage in the closed heterogeneous landscape, then we should not see an increase in bacteriophage adaptation on allopatric hosts in the closed homogeneous landscape, and this is what we found. In addition, we saw a decrease in infectivity of T7 with dispersal distance, which is consistent with the hypothesis that gene flow was driving the decrease in adaptation in the open heterogeneous landscape.

The variation in measures of adaptation that we found among replicates reflects the dynamical nature of the coevolving interaction, regardless of differences in productivity across the landscape (in the open communities; Forde et al. 2004). Gene flow further fuels ongoing change through the introduction of beneficial mutations, which can lead to higher levels of bacteriophage infectivity relative to those in the closed communities (Forde et al. 2004). Our results also indicate that bacteriophage infectivity may be more subtle than simple first- and second-

order host range mutants. To date, no research has looked beyond simple phenotypic changes in the coevolving pair (Chao et al. 1977; Forde et al. 2004). However, preliminary results indicate that mutations can occur in a number of different genes in *E. coli* in response to selection by T7 (S. E. Forde, unpublished data), similar to what has been found in T4-resistant mutants (Lenski 1988). Clearly, genetic variation in both the parasitoid and the host will shape the rate and dynamics of coevolutionary change (Nuismer and Doebeli 2004; Kopp and Gavrilets 2006). Future research will evaluate how different classes of mutations in the hosts influence counter-adaptation in T7 and elucidate the genetic mechanisms of infectivity and resistance in this coevolving interaction.

Past work testing for a decreasing relationship between adaptation of parasites to their hosts and dispersal distance has been equivocal; some past studies have found this relationship (Ebert 1994; Kaltz et al. 1999), while others have not or have at some spatial scales and not others (Thrall et al. 2002; Laine 2005, 2006; Hoeksema and Thompson 2007). Few studies, however, have explicitly addressed the underlying physical environment, and it is often assumed to be homogeneous. Interactions between dispersal distance and the abiotic environment become particularly important if dispersal of coevolving organisms occurs along an environmental gradient, as in source-sink metapopulations, similar to the experimental design described here (Hochberg and van Baalen 1998; Kawecki and Holt 2002). Therefore, the equivocal results of past work could be due in part to the environment in which the interaction is embedded. In some cases, abiotic factors may oppose biotic ones, whereas in other cases, they may reinforce adaptation to coevolutionary partners. In our open heterogeneous landscape, dispersal distance and the productivity gradient were correlated. However, because of our experimental design, we were able to evaluate how these forces countered one another to generate clinal patterns of adaptation of T7 to its host.

At first glance, it may not be surprising that gene flow reversed the effects of the productivity gradient in generating clines in bacteriophage adaptation since classic theory predicts gene flow to homogenize local populations (Slatkin 1973; Endler 1977). However, this should be the case only when gene flow is high. Recent research in which gene flow was directly manipulated suggests that low levels of gene flow can increase adaptation of parasitoids to their hosts (Forde et al. 2004; Morgan et al. 2005). Moreover, coevolutionary models have shown that the interaction of coevolutionary selection and gene flow can produce complex geographic mosaics of adaptation and maladaptation across heterogeneous landscapes (Hochberg and van Baalen 1998; Nuismer et al. 2000; Thompson et al. 2002*a*; Thompson 2005). Clinal patterns in adaptation will depend on the strength of the environmental gradient relative to gene flow (Nuismer et al. 2000). In the experiments described here, the fraction of immigrants (Slatkin's [1985] metric "m") ranged from 0.002 to 0.005 per generation (Forde et al. 2004). Thus, despite low levels of gene flow, we found that the movement of individuals could counter an underlying productivity gradient to produce clines in adaptation for this coevolving interaction, even when the gradients of gene flow and productivity are working in opposition.

The repeated occurrence of clines in adaptive traits that are correlated with environmental gradients has often been used to infer that selection pressures vary with distance (Kraaijeveld and Godfray 1999; Nuismer et al. 2000; Hare et al. 2005; Grahame et al. 2006). Not only do organisms have to deal with selection pressures generated by their environment, they must also evolve and coevolve with a myriad of other species, and these species interactions can also vary clinally (Kraaijeveld and Godfray 1999; Brodie et al. 2002; Toju and Sota 2006). Thus, patterns of adaptation of species to one another will be dictated by spatially variable selection imposed by abiotic and biotic factors, as well as by gene flow among populations (Thompson 2005). Understanding how these factors interact to shape patterns of adaptation is of particular importance as organisms are faced with new and changing abiotic and biotic environments, a scenario increasingly common as humans alter landscapes. Our results provide empirical evidence for the role that gene flow and environmental gradients have in generating geographic mosaics of coevolving interactions.

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