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A Quantitative Survey of Local Adaptation and Fitness Trade-Offs

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ABSTRACT: The long history of reciprocal transplant studies testing the hypothesis of local adaptation has shown that populations are often adapted to their local environments. Yet many studies have not demonstrated local adaptation, suggesting that sometimes native populations are no better adapted than are genotypes from foreign environments. Local adaptation may also lead to trade-offs, in which adaptation to one environment comes at a cost of adaptation to another environment. I conducted a survey of published studies of local adaptation to quantify its frequency and magnitude and the costs associated with local adaptation. I also quantified the relationship between local adaptation and environmental differences and the relationship between local adaptation and phenotypic divergence. The overall frequency of local adaptation was 0.71, and the magnitude of the native population advantage in relative fitness was 45%. Divergence between home site environments was positively associated with the magnitude of local adaptation, but phenotypic divergence was not. I found a small negative correlation between a population's relative fitness in its native environment and its fitness in a foreign environment, indicating weak trade-offs associated with local adaptation. These results suggest that populations are often locally adapted but stochastic processes such as genetic drift may limit the efficacy of divergent selection.

Keywords: genetic drift, genotype-by-environment interaction, local adaptation, natural selection, population divergence, reciprocal transplant.

Introduction

Adaptation by natural selection is the fundamental principle of the theory of evolution. It is particularly apparent at the species and higher taxonomic levels where similar selective environments have led to homoplasy (Sanderson and Hufford 1996) and where adaptive radiations have led to the rapid diversification of species (e.g., Levin 2000; Schluter 2000). An early step in the process of adaptation and diversification at higher taxonomic levels is differential adaptation of populations of the same species.

Adaptation at the population level can result in local adaptation. Results of reciprocal transplant experiments (Turesson 1922; Clausen et al. 1940) often show that genotypes are better adapted to their native environments than are genotypes from other populations (Linhart and Grant 1996; Van Zandt and Mopper 1998; Schluter 2000), but there are examples of populations that have relative fitness lower than that of foreign transplants (e.g., Rice and Mack 1991; Galloway and Fenster 2000; Hereford and Winn 2008) and evidence that despite stabilizing selection, populations are not at adaptive optima (Hansen et al. 2006). Furthermore, laboratory experiments have shown that genetic drift can limit a population's ability to adapt (Travisano et al. 1995) and can allow deleterious mutations to reach high frequency within populations (Lynch et al. 1999). That the ability to respond to selection depends on genetic variation within populations as well as gene flow between populations is well known (Hedrick 2000), yet many evolutionary models begin with the assumption that populations are at or near their adaptive optimum (Orzack and Sober 1994).

Theory suggests that the magnitude of local adaptation will increase with greater genetic variation within populations and with greater environmental and phenotypic divergence between populations (Lande 1976; Endler 1977; Slatkin 1985; Garcia-Ramos and Kirkpatrick 1997). Low genetic variation due to genetic drift can limit adaptation. Small populations may not be well adapted to their native environment because drift can make it difficult for advantageous alleles to reach high frequency (Whitlock 2003) or because genetic load due to the chance fixation of deleterious alleles leads to low fitness or extinction (Lynch and Gabriel 1987; Lande 1994; Whitlock et al. 2000). Gene flow can also prevent local adaptation by homogenizing allele frequencies and limiting the response to selection within environments (e.g., Stanton and Galen 1997; Hendry and Taylor 2004). Divergent selection leads to local

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adaptation when environmental heterogeneity is coarse grained relative to gene flow (Bradshaw 1984; Endler 1986), and local adaptation should be more pronounced between populations from more strongly divergent environments (Becker et al. 2006; Hereford and Winn 2008). Finally, phenotypic divergence can be correlated with local adaptation as a result of divergent selection on individual traits (de Jong 2005).

Local adaptation to one environment may cause lower relative fitness in alternative environments, resulting in a trade-off or cost of adaptation. These trade-offs are thought to maintain genetic variation among populations within species, leading to morphological or physiological specialization (Futuyma and Moreno 1988; Day 2000; Jasmin and Kassen 2007), and may promote ecological speciation (Rundle and Nosil 2005). The experimental evidence for fitness trade-offs is mixed, and theory suggests that adaptation and specialization can evolve in the absence of trade-offs (Fry 1996). Reciprocal transplant experiments offer a direct test of the hypothesis of costs of adaptation or fitness trade-offs (Bradshaw 1984; Schluter 2000). Reciprocal home site advantage indicates that adaptation to one environment comes at a cost of adaptation to other environments. Superior fitness of one population in both environments indicates adaptation without a fitness trade-off. Bennett and Lenski (2007) found that adaptation to alternate thermal environments in *Escherichia coli* was not associated with a trade-off in a third of their experiments. Yet there is evidence of fitness trade-offs associated with ecological speciation in natural populations (Rundle and Nosil 2005; Funk et al. 2006). An analysis of the reciprocal transplant literature can quantify the frequency and magnitude of trade-offs associated with adaptation of populations. If trade-offs are not common or are weak, then it can be concluded that adaptation is often not costly.

I performed a survey of published reciprocal transplant experiments to quantify the frequency and magnitude of local adaptation and the evidence for costs of adaptation. Previous quantitative surveys of local adaptation have focused on specific taxa or species interactions (Van Zandt and Mopper 1998; Hoeksema and Forde 2008) or alternate interpretations of local adaptation (Nosil et al. 2005), or they were limited to specific types of studies (Schluter 2000). Here I address four questions. First, how common and how strong is local adaptation? Second, does the magnitude of differences in the native environments of populations influence the degree of adaptation? Third, are populations that have undergone extensive phenotypic divergence more locally adapted than populations that have undergone less divergence? Finally, are there costs of local adaptation that could prevent a population from being well adapted to multiple environments?

Material and Methods

Literature Survey

I used search engines from ISI Web of Science and JSTOR to locate reciprocal transplant studies using the keywords "reciprocal transplant," "reciprocal transplants," "reciprocally transplanted," "local adaptation," and "egg transfer experiment." The search encompassed all studies that could be located in both search engines, up to those published through 2005.

Only studies that were conducted in natural field environments were included in the data set. I did not include laboratory or greenhouse studies because natural environmental variation provides the selective pressures responsible for local adaptation. I included only reciprocal transplant studies that measured fitness components directly based on viability and/or fecundity. Studies that used growth or biomass as fitness were not included, though they are fitness components for some clonal species. This selectivity was necessary so that differences between populations could be interpreted as differences in adaptation and so that organisms that differ in growth form (e.g., single celled vs. multicellular) or development could be compared.

The fitness components that I included were viability, fecundity, and a composite measure combining viability and fecundity. Viability was always survival, except in studies involving obligate parasites, for which I considered rate of infection to be the measure of viability. Traits that directly contribute to the number of offspring (e.g., number of eggs and number of seeds, flowers, or fruits) were considered fecundity. In some studies, measures of fecundity may also reflect viability selection if individuals that died before reproduction were assigned a fecundity of zero. In most studies I was not able to determine whether fecundity was calculated in this way. Measures of local adaptation quantified by the authors, using an index based on both viability and fecundity or demographic parameters estimating population growth rate, were defined as composite fitness.

Magnitude of Local Adaptation

I define the magnitude of local adaptation to be the difference in relative fitness between a native population and a nonnative population in the native's environment. This is the definition of local adaptation relevant to general theory of divergent selection, gene flow, and speciation (Endler 1977; Kawecki and Ebert 2004). Local adaptation defined in this way is not a measure of migration load (Lenormand 2002) because I am not comparing populations to some optimum they would achieve in the absence of migration. I considered each estimate of the difference

in relative fitness between two populations (or closely related species) at a site in a given year to be an independent observation because the definition of local adaptation assumes independent evolution of populations or demes within a species (Bradshaw 1984; Kawecki and Ebert 2004). I did not combine years within multiyear studies because in many studies, there were qualitative differences in the results for different years such that populations showed local adaptation in one year and local maladaptation in another (e.g., Rice and Mack 1991). Thus, averaging over years would obscure relevant variation within studies. Furthermore, the experimental methods often varied among years, or some populations were excluded from one year of the experiment and replaced by other populations. To account for variation between years, I included an effect of source population in some statistical models. Given that local adaptation is a population-level process and can vary among populations and years within a study, I chose population rather than published study as the appropriate unit of analysis.

For each study I recorded the mean fitness of each population at each field site. When available, I also recorded the sample size used to calculate the mean fitness. When mean fitness was not directly available, I used Data Thief 3 (Trummers 2005) to scan figures and estimate means. Most studies did not include variances of fitness components, making it infeasible to use meta-analytical methods that weight estimates by the their variances (Gurevitch and Hedges 2001). When studies provided unambiguous tests of statistical significance of the differences in relevant fitness components for specific pairs of populations, I recorded whether the difference in the mean fitness component was significant.

Environmental Differences and Phenotypic Divergence

To determine the effect of differences between the source populations' native environments on local adaptation, I recorded the values of up to four environmental variables measured at the individual field sites of the studies. An effort was made to record variables that were independent. For example, I would not include both soil moisture and annual rainfall if another variable that was unrelated to water availability was reported, but if only soil moisture and rainfall were available, I used both. To standardize measures of environmental variation among studies, I calculated Euclidean distances between all field sites within each study from the means of the environmental variables.

I recorded the values of up to four phenotypic traits of each source population at each field site to describe the magnitude of differences in mean phenotypes. If more than four traits were measured in the study, I chose traits that were least likely to be correlated. The most common types of traits were measures of size or growth. Few studies measured more than four unrelated traits. I compared the means of the traits of populations raised in the same field site to obtain a measure of phenotypic divergence that minimized the influence of environmental differences between populations' native field sites. I standardized the phenotypes of all populations by calculating Euclidean distances between the phenotypes of each pair of populations at each field site.

Fitness Trade-Offs

The frequency of fitness trade-offs can be measured by comparing the local adaptation of pairs of populations when raised in each other's native environments. If both populations have greater relative fitness in their native environments, I conclude that adaptation to one environment results in a cost of adaptation to the other environment. This measure of trade-offs is specific to a pair of populations. Therefore, a trade-off may be apparent when comparing populations A and B but not when comparing A and C.

Statistical Analysis

Statistical analysis required that I convert fitnesses of a variety of species from different kingdoms to relative fitness. I calculated relative fitness by dividing the magnitude of the fitness components of each population at a field site in a given year by the mean fitness at that site. In instances where both fecundity and viability had been measured in the same populations in the same year within a study, I multiplied viability and fecundity to provide an estimate of relative fitness that accounted for both components of fitness. This measure was used to estimate local adaptation in all analyses, except those that examined differences between viability, fecundity, and composite fitness components.

I considered one population locally adapted relative to another when it had equal or greater fitness in its native environment compared with that of the foreign population. An alternative definition is that local adaptation occurs when the native population has greater fitness in its native environment compared with that of a foreign population. I calculated the frequency of local adaptation using both definitions. The quantitative measure of local adaptation was the relative fitness of the native population at a field site in a given year minus the relative fitness of a nonnative population at that site,

$$\frac{W_{\text{population 1}} - W_{\text{population 2}}}{\overline{W}_{\text{site 1}}}, \tag{1}$$

where W represents the mean fitness components of the populations in the subscript at site 1 and $\overline{W}$ represents the mean fitness of all populations at site 1. This standardization of fitness components is equivalent to relative fitness calculated in analyses of phenotypic selection (Lande and Arnold 1983). The difference in relative fitness between nonnatives and natives is an estimate of selection against hypothetical migrants into a specific population. Positive values indicate selection against migrants (i.e., local adaptation), and negative values indicate that migrants would have greater fitness than would the native population (maladaptation of the native population). The frequency of local adaptation was calculated as the proportion of comparisons in which native populations had greater or equal fitness relative to that of nonnative populations at each transplant site in each year. I also calculated the frequency of local adaptation as the proportion of comparisons in which the native population had fitness greater than that of nonnative populations.

I used ANOVA to test the hypothesis that the magnitude of local adaptation differed for viability, fecundity, and composite fitness components. Linear regression was used to test the hypothesis that environmental and phenotypic differences were positively associated with the magnitude of local adaptation. Measures of viability where all individuals survived or died resulted in many instances of populations with equal fitness. Consequently, the distribution of magnitudes of local adaptation contained many zeros and was far from normal, prohibiting the use of parametric statistics or rank-based nonparametric methods of analysis. Therefore, I used a Monte Carlo simulation method to perform randomizations of the data (Cassell 2002). This method uses randomization to build a distribution of possible F values, calculated by reshuffling the observed combinations of dependent and independent variables across the entire data set. A separate F ratio is calculated for each randomization. This distribution of F ratios is used to calculate the probability of observing an F ratio more extreme than the F ratio calculated from the observed data. This probability is identical to the probability of a Type I error. This method is free from assumptions of normality and homoscedasticity because it compares F values instead of means. I used a program provided by Cassell (2002) in the SAS macro language (SAS Institute 2004) to perform this analysis. The distribution of F values was based on 1,000 iterations of the randomization. All P values associated with ANOVAs and regressions were calculated using this method.

To control for variation among source populations and to take into account multiple instances of the same source population, I included an effect of source population in tests of the effects of fitness component, environmental distance, and phenotypic distance on the magnitude of local adaptation. This effect was included in these models, along with the independent variables of interest, to determine whether adding source population to the models affected the qualitative interpretation of the significance test.

I quantified the magnitude of the overall fitness trade-off as the correlation between the difference in relative fitness of native and nonnative populations in the native's environment and the difference in the same populations in the nonnative's environment (as in Bennett and Lenski 2007). I used the bootstrap (Efron 1981) to calculate confidence intervals and P values of the correlation coefficient from 1,000 iterations using the SAS macro language (SAS Institute 2004).

Trade-offs may be stronger when environmental differences between populations are greater. I tested this hypothesis by performing a MANOVA of the effect of environmental distance between the native sites of populations on a focal population's relative fitness advantage in one environment and its advantage in the alternate environment. The MANOVA measured the effect of the magnitude of environmental differences on the correlation between fitness advantage in alternate environments. In other words, it measured the effect of environmental differences on the magnitude of the fitness trade-off between adaptation to alternate environments. This test is robust to departures from multivariate normality (Quinn and Keough 2002), and there was no significant heteroscedasticity between response variables. I used Pillai's trace to quantify the variance in trade-offs due to environmental distance (Quinn and Keough 2002, p. 431). The SAS procedure GLM (SAS Institute 1999) was used to perform this analysis.

Results

Literature Survey

The literature search yielded estimates from 74 studies (table A1 in the online edition of the *American Naturalist*), most of which focused on plants or animals (50 and 21 studies, respectively), although there were two studies of fungi and one of protists (with five species). The studies contained 1,367 measures of relative fitness, allowing calculation of 892 estimates of local adaptation (some populations were represented twice, with separate estimates of viability and fecundity).

Magnitude of Local Adaptation

Inspection of the plot of sample size (number of individuals of each source population at each site) versus degree of local adaptation shows little evidence of publication bias

against studies with small sample sizes that do not find local adaptation (fig. 1). The figure gives no indication of a normal distribution or convergence of effect size to the mean effect size with increasing sample size. Not all estimates of local adaptation are represented in figure 1 because not all studies provided clear descriptions of the sample size for individual mean fitness components at each site in each year. For the studies that provided sample sizes, there was no correlation between magnitude of local adaptation and sample size ($\rho = -0.04$, $P > .05$, $N = 609$). The correlation remained nonsignificant for absolute value of local adaptation ($\rho = -0.06$, $P > .05$, $N = 609$). In addition, when estimates of local adaptation were weighted by their sample size, there was only a slight difference between weighted (0.37 ± 0.03 SE) and nonweighted (0.39 ± 0.03 SE) means.

Many estimates of the magnitude of local adaptation were large and negative, indicating that the native population had fitness lower than that of nonnative populations (fig. 1). Of the 74 studies, 43 reported levels of statistical significance of the relevant fitness components for the comparisons between individual pairs of populations. Among these studies, 21% of the negative estimates were significant, and 54% of the positive values were significant.

Local adaptation was greater when quantified by composite fitness or fecundity than when viability was the fitness measure (fig. 2). Both composite and fecundity measures of fitness resulted in stronger local adaptation than did viability. The difference between fecundity and viability was marginally significant ($P = .053$).
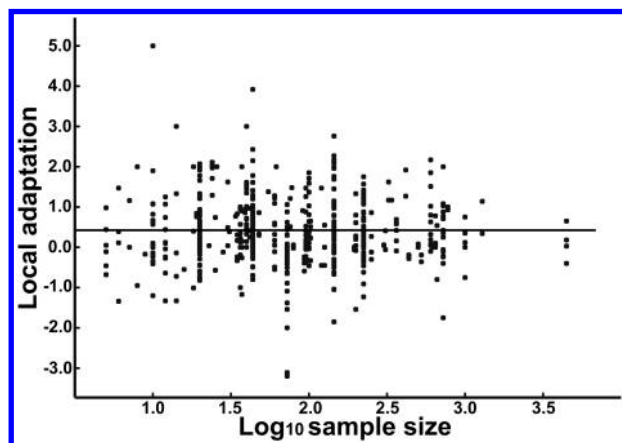

Figure 1: Funnel plot of the relationship between magnitude of local adaptation and sample size. Magnitude of local adaptation is calculated by subtracting the immigrant's relative fitness from the native population's relative fitness in the native's environment. Values that are greater than or equal to 0 indicate local adaptation. The mean local adaptation is given by the horizontal line. Note that this figure includes only the estimates with published sample sizes.
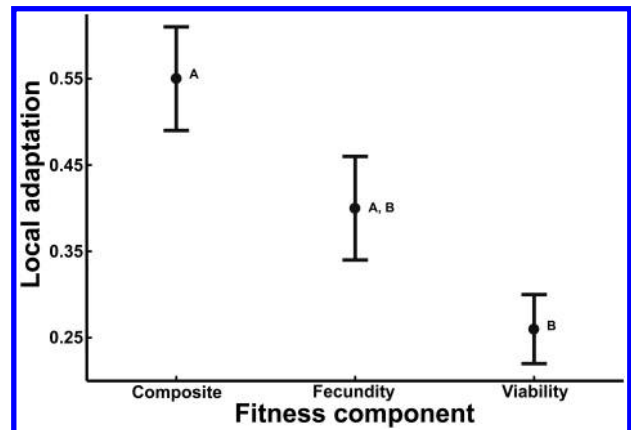

Figure 2: Mean magnitude of local adaptation for three fitness components. Error bars are 1 SE. Means that share the same letter are not significantly different. Statistical significance calculated from randomization method.

Combining viability and fecundity fitness components for populations in which both were estimated yielded 777 estimates of local adaptation. The overall magnitude of local adaptation was 0.45 ± 0.04 SE, meaning that native populations had, on average, 45% greater fitness than did foreign populations. The frequency of local adaptation was 0.71 ± 0.02 SE if native populations were considered locally adapted when they had equal or greater relative fitness compared with that of nonnative populations. The frequency was 0.65 ± 0.02 SE if local adaptation is defined as greater relative fitness of native populations. All analyses described below were performed on either composite fitness components or the product of viability and fecundity when both were available. When only viability or fecundity was available, that fitness component was used.

Environmental Differences and Phenotypic Divergence

Environmental variables in the studies were represented by physical features such as elevation and biotic factors such as the frequency of predation (table A1). Of the 74 studies, 36 quantified some feature of the environment. There were 290 measures of environmental distance between native sites in the data set, and the mean distance was 1.75 ± 0.12 SE. There was a significant positive regression of local adaptation on environmental distance, but the regression explained little variance in local adaptation ($\beta = 0.12$, $P = .0030$, $R^2 = 0.04$; fig. 3). The significance of the regression was not driven by large values of local adaptation and environmental distance. Removing local adaptation values greater than 5.0 and environmental distance values greater than 6.0 increased the slope from
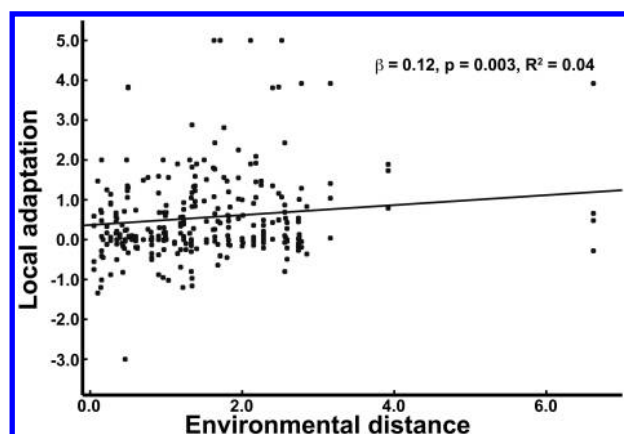
Figure 3: Regression of local adaptation on environmental distance between sites in reciprocal transplant studies. The distance measures are Euclidean distances for environmental data gathered from individual studies.

0.12 to 0.27, and the regression was highly significant ($P < .0001$).

The phenotypic characters measured in the studies were primarily size-related traits such as growth rate or biomass and life-history traits associated with timing of reproduction (table A1). Of the 74 studies, 44 included phenotypic measurements. The mean phenotypic distance between native and foreign populations was 0.52 ± 0.04 SE, based on 304 estimates. The regression of local adaptation on phenotypic distance was not significant and explained almost no variation in local adaptation ($\beta = 0.03$, $P = .658$, $R^2 = 0.0005$; fig. 4).

Measures of environmental variables and phenotypic traits were unavailable for many populations and species. This lack of data precluded simultaneous tests of relationship of both factors to local adaptation because the sample sizes for the tests were low, making it difficult to determine whether lack of a statistical relationship was due to low power or to a genuine lack of an effect.

Fitness Trade-Offs

Fitness advantages in the native environment were sometimes associated with fitness disadvantages in nonnative environments. Almost half of the comparisons between populations showed evidence of a trade-off (fig. 5). The upper left quadrant of figure 5, indicating populations that had a fitness advantage in their native site and a disadvantage in foreign sites, contains 48% of the data. The points in the lower left and upper right quadrants of figure 5 show cases in which one population had greater fitness in both environments, and these contain 43% of the data. The lower right section shows the examples where both

populations had a disadvantage in their native environment. The correlation between a population's relative fitness in its native environment and its relative fitness in the alternate environment was negative and significant. The magnitude of the correlation was small ($\rho = -0.14$, $P = .01$, $N = 360$), but the confidence interval of the correlation did not include 0 (-0.03, -0.27).

Environmental distance influenced the magnitude of trade-offs. The MANOVA of environmental distance on fitness differences in two environments showed a significant effect of environmental differences between sites (Pillai's trace $= 0.074$, $F = 5.60$, df $= 2, 140$, $P = .0017$).

Including the effect of source population in statistical tests of the differences among fitness components, the effect of environmental distance on local adaptation, and the effect of phenotypic distance on local adaptation changed the qualitative outcome of only one test. The difference between the magnitude of local adaptation measured as viability and as fecundity changed from marginally significant to nonsignificant.

Discussion

The survey of the literature suggests that local adaptation is common and that, on average, a local population has 45% greater fitness than a foreign population. The lack of a relationship between sample size and local adaptation suggests little publication bias against studies with small sample size that do not report local adaptation. The magnitude of differences between the home environments of populations in reciprocal transplant studies had a small but significant positive effect on the magnitude of local
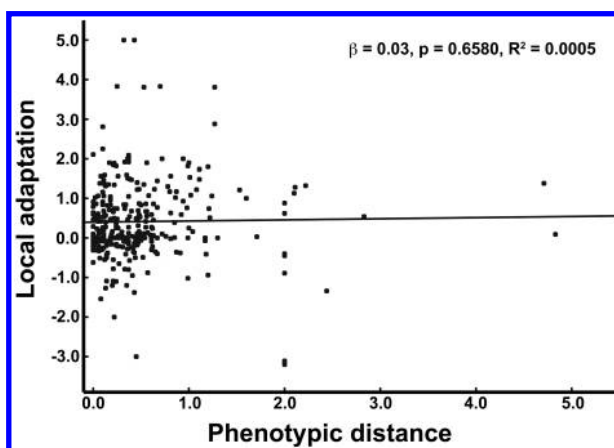

Figure 4: Regression of local adaptation on phenotypic distance between populations in reciprocal transplant studies. The phenotypic distances are calculated from Euclidean distances of phenotypic trait means for each population.
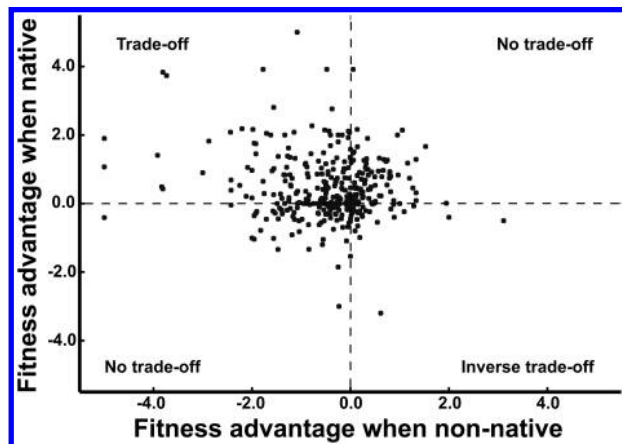
Figure 5: Plot of a population's fitness advantage at its native site and its fitness advantage at the immigrant's native site. Fitnesses are relative to the mean fitness at each site. Each point shows the difference in relative fitness between a pair of populations at each population's home site in a given year. The quadrants, indicated by dashed lines, separate alternative qualitative outcomes of reciprocal transplant experiments. The upper left corner shows examples where both populations had greater fitness in their native environments (reciprocal local adaptation). The upper right corner gives examples where the focal population had greater fitness at its home site and at the foreign site. The lower left corner shows examples where the focal population had lower fitness at its native site and in the foreign site. The lower right shows the outcomes of experiments where each population had lower fitness in its native environment.

adaptation, suggesting that greater local adaptation results from greater differences between environments. Phenotypic differences between populations were not associated with the magnitude of local adaptation. Finally, local adaptation often resulted in trade-offs, though the magnitude of the cost of local adaptation was small.

The data analyzed here are not drawn from a random sample of populations. They were gathered from studies in which the authors often had an a priori expectation of local adaptation, with many reciprocal transplants conducted across continents or along steep elevational gradients, well beyond the average dispersal distance of the study organism. The data most likely constitute a sample biased toward populations that are expected to have undergone extensive divergence. Thus, if there is a random distribution of local adaptation in nature, the frequency and magnitude reported here are likely to be overestimates. Similarly, the strength of trade-offs or costs of adaptation estimated here are likely to be greater than in a random sample of populations.

Magnitude of Local Adaptation

The average magnitude of local adaptation depended on the measure used to quantify fitness. Local adaptation measured with viability as fitness was smaller than with fecundity or composite fitness (fig. 2), suggesting that the overall magnitude of local adaptation would have been greater had more studies included fecundity or a composite measure of fitness. Viability selection on phenotypic traits is often estimated to be weaker than fecundity selection (Kingsolver et al. 2001; Hereford et al. 2004). Viability selection and local adaptation based on viability may be weaker because there is less variance in viability than in fecundity or other fitness measures. Because organisms have to survive to reproductive age in order to produce offspring, fecundity or population growth may capture more of the underlying variation in fitness, resulting in more accurate estimates of selection and local adaptation. Alternatively, past selection may have eliminated variation in traits that influence survival, resulting in little contemporary viability selection. Future studies should include the most comprehensive measure of fitness possible, given that the fitness metric influences the interpretation of experiments.

Given strong selection and ample additive genetic variation, populations are expected to quickly adapt to their native environments (Hendry and Kinnison 1999), suggesting that foreign population advantage should be rare. However, the frequency of maladapted populations reported here suggests that foreign population advantage may not be rare. It appears that selection acts on most measurable phenotypic traits (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001) and can often be exceptionally strong (Hereford et al. 2004). Other reviews have shown that there is additive genetic variation within most natural populations (Mousseau and Roff 1987; Roff and Mousseau 1987; Houle 1992; Geber and Griffen 2003) and that new variation is continually introduced via mutation (Houle et al. 1996). The high frequency of local maladaptation suggests that stochastic processes such as genetic drift often limit local adaptation (e.g., Travisano et al. 1995).

While the results suggest that genetic drift often limits local adaptation, it is doubtful that gene flow alone explains the frequency of maladapted populations (fig. 1). I considered populations locally adapted if native and foreign populations had equal fitness yet there were many examples of significant local maladaptation. Gene flow would prevent local maladaptation because populations would have equal fitness in one or both environments. Gene flow could cause local maladaptation if gene flow from a third population prevents adaptation of one of the focal populations (e.g., Lenormand 2002). Even with limited gene flow and assuming negligible genetic drift, beneficial alleles are expected to quickly spread among populations (Slatkin 1976, 1985). If alleles can spread readily throughout the species range (e.g., McDaniel and Shaw 2005), then gene flow can prevent populations within a

species from evolving as independent units. In their review of gene flow and selection on quantitative trait loci, Morjan and Rieseberg (2004) concluded that in most instances, levels of gene flow were high enough and/or selection on individual loci was strong enough to allow advantageous alleles to spread throughout a species' range. The frequency (0.29 or 0.35, depending on definition) and magnitude (−0.47) of local maladaptation reported here suggest that mutually beneficial alleles often cannot or have not spread between populations. Thus, gene flow may not be a strong cohesive force for at least some organisms.

In addition to genetic drift, other factors could result in local maladaptation. First, environmental maternal effects may result in the appearance of local maladaptation because individuals whose parents were raised in low-resource environments may be at a fitness disadvantage in any environment. For each study, I recorded whether maternal effects were controlled. Though there was no significant effect on local adaptation when maternal effects were controlled (J. Hereford, unpublished data), few studies controlled for maternal effects. The lack of an effect may result from lack of statistical power due to low sample size. Second, the genetic variance/covariance structure within populations may prevent adaptive responses to selection over short time periods. If there are significant opportunities for migration and outcrossing, over time gene flow should allow the more adaptive covariance structure to invade or provide the genetic variation required to respond to selection (Kirkpatrick and Barton 1997; Guillaume and Whitlock 2007).

In host-parasite interactions, natural selection is expected to result in a pattern where parasites may be better able to infect hosts from foreign populations because foreign hosts have not evolved resistance (Kaltz et al. 1999; Gomulkiewicz et al. 2000; Thompson 2005). A large number of estimates of fitness derived from host-parasite interactions (including predator-prey and insect-herbivore interactions) could explain the frequency of maladaptation in the data. Removing the 13 studies and 56 estimates in my data set that are from host-parasite systems changed the mean frequency of local adaptation from 0.71 to 0.70, and the average magnitude of local adaptation declined from 0.45 to 0.44. These minor effects suggest that coevolutionary interactions do not drive the frequency of local maladaptation.

Environmental Differences and Phenotypic Divergence

The small amount of variation in local adaptation explained by environmental and phenotypic differences suggests that it may sometimes be difficult to identify the environmental gradients on which local adaptation occurs or that differences in the expression of phenotypic traits

may not be associated with differences in relative fitness. I found that environmental and phenotypic divergence explained little variation in the magnitude of local adaptation (figs. 3, 4). Though environmental variation is not a direct measure of divergent selection, stronger environmental differences might be expected to result in more divergent selection (e.g., Schluter and Grant 1984), and divergence between populations in at least some phenotypic traits should be associated with local adaptation (de Jong 2005). Many of the phenotypic traits in the data were related to size, which is often positively correlated with fitness (Kingsolver et al. 2001; Hereford et al. 2004). The lack of a significant relationship between local adaptation and phenotypic divergence may not be due to a lack of selection on these traits. Instead, differences in the expression of these traits may not contribute to differences in relative fitness. Individuals may be able to grow to large sizes in novel environments but may not be able to get the same fitness benefit from large size in novel environments that they could gain in their native environment. I treated the traits and environmental variables within each study equally. If traits or variables differed in their effects on local adaptation, I could have obscured the effects of important factors by including unimportant variables in the Euclidean distance measures. Alternatively, traits that confer local adaptation are complex, and variation in local adaptation cannot be explained by a small number of traits or environmental factors.

Fitness Trade-Offs

Costs of adaptation or adaptive trade-offs do not appear to be strong enough to prevent simultaneous adaptation to multiple environments. The correlation between a population's relative fitness in its native environment and its relative fitness in a foreign population's environment was significant but weak ($\rho = -0.14$; fig. 5). One of the underlying assumptions in the theory of the evolution of specialist phenotypes is that specialists suffer a cost, in that they cannot be well adapted to alternate environments or resources (Lynch and Gabriel 1987; Futuyma and Moreno 1988). Weak costs of adaptation may explain why the predictions of theory relating evolution of specialization to costs of adaptation are frequently not met (Futuyma and Moreno 1988). There are examples of strong costs of adaptation and specialization associated with intraspecific competition (Schluter 1995; Losos et al. 1997), but I did not specifically test that theory here.

Trade-offs associated with local adaptation were stronger when environmental differences between populations' native sites were larger. The significant effect of environmental difference in the MANOVA suggests that costs of adaptation will increase when a population adapts to en-

vironments that are drastically different from its ancestral environment. Hughes et al. (2007) describe a similar pattern in which the presence of trade-offs is environment dependent. In their study, adaptation always led to trade-offs when bacteria adapted to the lowest pH, but trade-offs were present only one out of five times when adapting to a pH treatment that was more similar to the ancestral pH.

Conclusions

This study shows that local adaptation is common but that many populations may be prevented from adapting to their local environment. This study also confirms theory that has shown that adaptive divergence not only depends on environmental differentiation and limited gene flow but also may be influenced by genetic drift. Studies that do not demonstrate local adaptation should not be looked on as failed experiments but as demonstrations that populations may be prevented from reaching adaptive optima. Future reciprocal transplant experiments should explicitly investigate the mechanisms that inhibit local adaptation. Further investigation of the genetics and ecology of maladapted populations will provide a richer understanding of the process of adaptation (e.g., Crespi 2000).

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