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Author(s): Deepa Agashe
Source: *The American Naturalist*, Vol. 174, No. 2 (August 2009), pp. 255-267
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/600085
Accessed: 18/06/2015 14:41

VOL. 174, NO. 2 THE AMERICAN NATURALIST AUGUST 2009 Ⓔ

The Stabilizing Effect of Intraspecific Genetic Variation on Population Dynamics in Novel and Ancestral Habitats

Deepa Agashe*

Section of Integrative Biology, University of Texas, Austin, Texas 78712

Submitted November 3, 2008; Accepted February 13, 2009; Electronically published June 11, 2009

Online enhancement: appendix.

ABSTRACT: Recent studies show that intraspecific genetic variation in asexual species may have large effects on community and ecosystem functions, increasing their stability, productivity, and species richness. However, major questions regarding its population-level impact remain empirically unanswered: (*a*) How does intraspecific genetic diversity affect the ecological characteristics of sexual species, in which recombination can alter the outcome of causal mechanisms such as selection and niche diversification? (*b*) Does genetic diversity increase population dynamic stability? (*c*) Is the impact of genetic diversity dependent on the selective environment? To answer these questions, I founded replicate flour beetle (*Tribolium castaneum*) populations with different degrees of ecologically relevant, heritable trait variation and monitored their dynamics for approximately eight generations. I show that population stability and persistence increased with greater genetic variation but that the stabilizing effect was independent of the selective habitat (different proportions of ancestral and novel resources). Alleles from a single founding strain underwent a selective sweep in the homogeneous ancestral habitat but not in a novel heterogeneous habitat. These results expand current understanding of the ecological impacts of genetic diversity by showing that genetically more diverse sexual populations persist longer and are more stable but that the selective environment determines the mechanistic basis of increased stability.

Keywords: population stability, intraspecific variation, genetic diversity, selection, extinction, habitat heterogeneity.

Introduction

Biologists have long known that heritable trait variation within populations is critical for evolutionary processes such as adaptation. While the evolutionary impacts of genetic variation are well understood, it is only during the past decade that we have begun to document the pervasive ecological impacts of standing intraspecific genetic variation (reviewed in Hughes et al. 2008). For instance, intraspecific genetic diversity enhances population persistence (Newman and Pilson 1997; Vilas et al. 2006), colonization success (Gamfeldt et al. 2005), growth (Pelletier et al. 2007), productivity (Bell 1991; Smithson and Lenne 1996), and resistance to invasion (Crutsinger et al. 2007) and pathogens (Pearman and Garner 2005). In social insects, it enhances group performance (Jones et al. 2004; Mattila and Seeley 2007) and disease resistance (Tarpy 2003); it allows for coexistence in predator-prey systems (Imura et al. 2003; Yoshida et al. 2003) and increases growth rates of metapopulations (Hanski and Saccheri 2006). Finally, genetic diversity enhances many important community and ecosystem functions (Booth and Grime 2003; Hughes and Stachowicz 2004; Reusch et al. 2005; Crutsinger et al. 2006; Johnson et al. 2006; Lankau and Strauss 2007; Hajjar et al. 2008).

Drawing on community diversity-stability concepts (Tilman 1999; Loreau 2000), Hughes et al. (2008) have proposed two types of mechanisms to account for these observed positive effects of genetic diversity. Additive effects are said to occur when measured population functions can be attributed directly to the properties and frequencies of constituent genotypes in monoculture. For example, the mean productivity of high-diversity populations (containing more genotypes) may be greater because they are more likely to contain more productive genotypes (the "sampling effect"; note that this is a statistical effect, independent of similar consequences of natural selection described next). Genetic diversity may also have nonadditive effects whereby population functions are an emergent property of interactions between constituent genotypes. One example is natural selection, which can drive a particular high-fitness genotype to fixation in a population and thereby increase the mean productivity of high-diversity assemblages. Another nonadditive effect can arise from niche complementarity, whereby genotypes either occupy different niches or facilitate growth of other genotypes, increasing the net productivity of genotype mixtures. Empirical evidence (reviewed in Hughes et al.

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* E-mail: dagashe@oeb.harvard.edu.

Am. Nat. 2009. Vol. 174, pp. 255–267.
DOI: 10.1086/600085

2008) supports all these mechanisms, which are not necessarily mutually exclusive.

To date, studies of the ecological impacts of genetic variation (cited above) have used different clones or unique nonrecombining genotypes—often plants—to create different levels of genetic diversity in experimental populations. These studies thus effectively tested whether the community- and ecosystem-level impacts of intraspecific diversity are analogous to the well-known consequences of species diversity. Their limitation, therefore, is that they fail to consider a critical feature that distinguishes intra- and interspecific variation: sexual recombination among individuals generates novel allele combinations. Indeed, a recent review of the ecological effects of intraspecific diversity notes that the ecological consequences of genetic variation within sexual species remain an open question (Hughes et al. 2008). Mechanisms responsible for impacts of increased genetic diversity in sexual species may include selection on novel allele combinations, in addition to selection for specific alleles from founding genotypes. Whereas novel beneficial allele combinations arise from sexual reproduction, sexual recombination also breaks up existing advantageous combinations, altering the efficacy and speed of selection. It is thus unclear, a priori, whether the ecological consequences of intraspecific diversity would be stronger or weaker in sexual compared to asexual species.

Previous studies have also largely neglected the impact of intraspecific genetic variation on population stability, which is an important predictor of population persistence. Recent theoretical models show that population stability can be enhanced by heritable trait variation among individuals (e.g., Bjornstad and Hansen 1994; Doebeli and de Jong 1999; Jager 2001; Fox 2005). Specifically, a one-locus, two-allele population genetic model incorporated genotype-specific responses to population density to simulate genotype-specific variation in density dependence. In each generation, the relative fitness of genotypes was used to determine the distribution of a heritable trait (response to population density; Doebeli and de Jong 1999). The model shows that incorporating such heritable variation in sensitivity to density dependence can simplify population dynamics and increase population stability. This result makes intuitive sense: consider population size fluctuations caused by over- and undershooting of the carrying capacity due to strong density dependence. If individuals vary in the degree to which high population density affects their fecundity, populations are less likely to over- or undershoot their carrying capacity, mitigating extreme fluctuations in population size. However, we lack empirical tests of this theoretical prediction that heritable intraspecific variation stabilizes population dynamics.

Expression of heritable variation often varies with the selective environment in both laboratory and natural populations (for reviews, see Hoffmann and Merilä 1999; Charmantier and Garant 2005), and the impacts of reduced genetic variance due to inbreeding are also more severe in stressful habitats (Frankham et al. 2002; Armbruster and Reed 2005). Hence, the impact of intraspecific genetic variation on population characteristics such as population stability is likely to be habitat dependent. Furthermore, the likelihood of niche diversification increases with temporal or spatial environmental variation (e.g., Rainey and Travisano 1998; Day 2000; Kassen 2002 and references therein), and therefore the mechanistic basis of the observed impacts of genetic diversity may also be habitat dependent. Previous studies did not explicitly address the environmental context or test for an interaction effect of genetic variation and environment on the measured population or community properties (but see Gamfeldt and Kallstrom 2007, in which population size predictability across replicates was a function of both the degree of environmental perturbation and genetic diversity). Thus, we have limited empirical evidence to evaluate whether the selective environment shapes the ecological impacts of genetic diversity.

Here I present the results of an experiment to address the aforementioned gaps in our understanding of the population-level ecological impacts of genetic variation. I manipulated founding genetic variation in replicate laboratory populations composed of freely interbreeding strains of the red flour beetle *Tribolium castaneum*. Populations were maintained in three different habitat treatments: one containing only the ancestral resource (wheat flour), a second composed of adjacent patches of the ancestral and a novel resource (corn flour), and a third habitat containing only the novel corn resource. Flour beetle populations are regulated by negative density dependence (Sokoloff 1977) and exhibit additive genetic variation and gene-by-habitat interaction for critical traits such as resource use, degree of egg cannibalism, fecundity, and egg-to-adult viability (Via 1991; Via and Conner 1995). Substantial among-strain phenotypic variation for fitness-related traits on corn and wheat flour (table 1) indicates that genetic variation could have a detectable impact on population growth dynamics in different habitats. The results of this experiment show that genetic diversity increases population stability in all selective environments but that the mechanistic basis of this stabilizing effect is habitat dependent.

Methods

Beetle Stocks and Maintenance

Tribolium castaneum is a global pest that both inhabits and eats various cereals. The Beeman lab (Biological Research

Table 1: Among-strain trait variation

Strain	Fecundity (eggs female^{-1} day^{-1}; $n = 36$ females)		% egg survival ($n = 150$ eggs)		% larvae choosing corn patch ($n = 46$ larvae)
	Wheat	Corn	Wheat	Corn	
Col-2	16.25 ± 4.80	1.5 ± .65	100.00 ± .00	85.70 ± .03	43.48 ± .07
Pak-3	19.80 ± 3.08	5.4 ± 1.29	100.00 ± .00	54.45 ± .04	15.21 ± .05
Z-7	8.33 ± 1.67	1.0 ± .58	86.65 ± .03	61.65 ± .04	13.04 ± .05
Tiw-5	18.60 ± 1.54	1.4 ± 1.17	87.35 ± .03	6.75 ± .02	34.78 ± .07

Note: Mean values (± standard error) are shown for each trait, measured for isolated individuals of each of the four experimental strains; n indicates the sample size for each strain (and flour type, where applicable).

Unit, Grain Marketing and Production Research Center, Kansas) has maintained numerous stock populations of this species on wheat flour (+5% yeast) under laboratory conditions for ~20 years (~250 generations). For my experiments, I obtained four of these strains (Col-2, Pak-3, Z-7, and Tiw-5), originally collected from geographically different source populations. I maintained stock and experimental populations in laboratory incubators in 95% wheat flour + 5% yeast (henceforth "wheat") at 33°C (±1°C) and 70% relative humidity. Organically produced flour was obtained from a single supplier throughout the experiment. I allowed stock populations to adjust to local lab conditions for 6 months before starting experiments.

Among-Strain Trait Variation

While geographically and temporally isolated populations will accumulate neutral genetic variation, they could potentially retain common ancestral trait values and lack heritable variation for ecologically important traits. To test whether the four experimental strains differed in traits relevant to population growth in different habitats, I quantified three traits for each strain: fecundity and egg-to-adult survival in wheat and in corn flour and behavioral preference for flour type. To quantify fecundity, I randomly picked sexually mature, mated females from stock populations of each strain. Females were confined singly in 1-mL plastic vials (to prevent confounding effects of egg cannibalism) in equal amounts of either wheat or corn flour. Fecundity was measured as the number of eggs laid per female per day, averaged over 3 days. To measure strain-specific survivorship, eggs from females of each strain were pooled, and individual eggs were isolated in 0.5-mL vials containing either wheat or corn flour. Each vial was checked weekly, adding fresh flour each time, until eggs/larvae were dead or had eclosed successfully into adults. To measure behavioral resource preference, ~3-week-old larvae were picked randomly from stock populations and placed in the center of 35-mm test petri dishes, with one larva per petri dish. Each petri dish contained adjacent patches of equal amounts of wheat and corn flour. The presence/absence of the larva in each flour patch was noted after 24 h as an indicator of behavioral resource choice. Visible burrows made by larvae while moving in the flour showed that larvae typically sampled both flour patches before settling in one patch.

Experimental Populations

I initiated experimental populations in a staggered manner over 3 months, with 120 randomly picked adult beetles from stocks (table 2). All stocks had an ~1 : 1 sex ratio (based on sexing 50 adults per stock); hence, all experimental populations likely received equivalent numbers of females. I created four levels of genetic variation, using varying proportions of each of the four strains, with the assumption that sexual reproduction between strains would lead to increased diversity. Replicate populations with the lowest level of genetic variation (single-strain populations) were founded using 120 adults of Col-2, Pak-3, Z-7, or Tiw-5 strains. Populations with the next level of genetic variation (two-strain populations) were founded using 60 adults per strain for each of the six possible two-strain combinations. Populations with the third-highest level of variation (three-strain populations) were founded using 40 individuals per strain for each of the four possible three-strain combinations. Populations with the highest level of genetic variation were founded by mixing 30 individuals from each of the four strains. I chose to maximize accuracy with five replicates per strain combination for the highest and lowest levels of genetic variation and two replicates each for intermediate levels of genetic variation (table 2). I created three different resource/habitat treatments: one containing 50 g wheat flour, one with 25 g each of wheat and corn flour in adjacent patches and allowing free movement between resources, and the third with 50 g corn flour. Two single-strain populations in the wheat treatment, one in the wheat + corn treatment, and two from the corn treatment were accidentally spilled or mixed during the study, decreasing the number of repli-

Table 2: Experimental design

Genetic variation (no. founding strains)	Possible strain combinations	Individuals/ strain	Replicates/ combination	Total populations
Least (1)	4 (C/P/Z/T)	1	5	20
Low (2)	6 (CP/PZ/ZT/CT/CZ/PT)	.5	2	12
Intermediate (3)	4 (CPZ/PZT/CPT/CZT)	.33	2	8
High (4)	1 (CPZT)	.25	5	5

Note: *Tribolium castaneum* strains are denoted C (Col-2), P (Pak-3), Z (Z-7), and T (Tiw-5). This design was used for each of the three habitat types (wheat only, corn only, or wheat + corn).

cates of the relevant strains to three or four instead of the original five replicates.

I censused each population every 2 weeks for a total of 16 census points, or approximately eight overlapping generations. During a census, I counted larvae, pupae, and adults in each flour patch within a container and discarded dead beetles. I replaced the used flour with fresh flour and returned larvae and pupae to the same flour type in which they were found (wheat or corn). Before discarding dead beetles and used flour, I froze them at −80°C for 24 h to prevent accidental spread of the pest species.

Tribolium castaneum populations maintained under continuous overlapping generations (as in this experiment) are regulated by density-dependent traits such as egg cannibalism, fecundity, and adult and larval mortality (Sokoloff 1977; see fig. A1 in the online edition of the *American Naturalist* for larval and adult dynamics in this experiment). Because adult life span is longer than the typical egg-to-adult development time, adult numbers remain relatively constant after an initial increase, while the number of larvae fluctuate, depending on resource quality, resource renewal rate, and larval development time (Mertz 1972; Sokoloff 1977), all of which are affected by habitat and genotype (e.g., see table 1). Therefore, detailed stage-structured dynamics and life-history changes during this experiment will be addressed in a separate paper (D. Agashe, unpublished manuscript). For the current analysis, I use the number of adult beetles to estimate population size and stability because this number is a straightforward measure of overall population performance and productivity.

Data Analysis

Population Persistence. Counts of extinct populations were analyzed as a function of genetic variation and habitat using a generalized linear model (proportion extinct populations = genetic variation × habitat) with binomial errors. The Akaike Information Criterion (AIC) was used to evaluate model fit and find the minimal model that best described the data. In addition, I used Fisher's exact tests to test for a significant effect of genetic variation on the proportion of populations that became extinct during the study in each habitat. All analyses were conducted in R (R Development Core Team 2008).

Population Stability and Size. Various measures and definitions of population stability have been used in the ecological literature (Gaston and McArdle 1994; Grimm and Wissel 1997). I quantified temporal variability in the adult population size (coefficient of variation in size, CV) as the most noninvasive and direct measure of stability for my experiment. Quantifying other stability measures, such as resistance to perturbation, would have interfered with my aim of analyzing the impact of founding genetic variation. Since populations in the corn-only treatment either became extinct or declined rapidly during the experiment, data from this habitat were not analyzed for stability. All stability and size analyses therefore refer only to the wheat and wheat + corn treatments.

Results from an ANOVA may be unreliable for this study because the experimental design was unbalanced. This was due to the combinatorics inherent in manipulating genetic variation: there were four, six, four, and one data points (corresponding to 15 strain combinations) within each level of genetic variation (table 2). Furthermore, strain combinations within each level of genetic variation were unique. Therefore, I analyzed the data as described below for population CV as the response variable. Identical steps were taken to test for an effect of genetic variation on mean population size.

1. I fitted a linear model (CV = −1 + strain combination + habitat × strain combination) to the data, with habitat and strain combination as factors (excluding data for extinct populations). Each strain combination was replicated two to five times, and there was no significant heteroscedasticity; hence, this parametric model fitting was valid.
2. I extracted the effect estimates and associated standard errors for each strain combination in each habitat. I used these values to calculate the average effect size for strain combinations within a given level of genetic variation and the variance of this estimate. For each habitat, I thus obtained four values corresponding to the effect size of each level of genetic

variation and four values for the associated variance. I fitted a weighted linear regression model to these data (weighted by the variance of effect estimates) to test whether population CV varied as a function of genetic variation.

3. To determine whether the impact of genetic variation on population CV was habitat specific, I tested whether the slope of the regression line was significantly different between the two habitats, using a *t*-test. Similarly, to test for a significant effect of habitat on population CV, I tested whether the intercept of the regression line was significantly different between the two habitats.

Testing for Selective Fixation of Alleles. For each habitat, I used two tests to determine whether the selective sweep(s) of allele(s) from a single founding strain was responsible for increased population stability and size. First, for each strain in turn, I categorized all experimental populations on the basis of the fraction of founding adults belonging to that strain (table 2). When populations with no individuals of the focal strain were excluded, each population was thus composed of 25%, 33%, 50%, or 100% individuals of each strain. I used a linear model to test for a significant regression between CV/population size and the fraction of individuals of the focal strain. A significant regression with a positive slope would indicate a selective sweep of alleles of the focal strain. Second, I calculated pairwise Tukey HSD contrasts for population CV (or size) between all single-strain and high-diversity populations in wheat and wheat + corn habitats. The number of replicates in each case was similar (five initially, or three after extinction), and there was no significant heteroscedasticity (Bartlett's test for homogeneity of variances, $P > .05$). A selective sweep of alleles from a founding strain would be indicated if the size and stability of one of the single-strain populations were higher than that of other single-strain populations and equivalent to that of the high-diversity populations.

Results

Among-Strain Trait Variation

Results from assays of three different traits show significant among-strain variation for fecundity and survival in wheat and corn flour, as well as behavioral preference for corn flour (table 1). Strains with greater fitness in wheat flour (Pak-3 and Tiw-5) performed relatively poorly in corn flour, while ~45% of larvae of strain Col-2 preferred corn over wheat flour, and 85% of Col-2 eggs survived to adulthood in corn. However, Col-2 females had very low fecundity in corn. These results highlight two important points. First, the experimental strains varied in fitness-related traits (survival and fecundity; both are highly heritable traits in *Tribolium castaneum*) and behavioral resource preferences (unknown heritability), traits that can alter population dynamics. Second, no single strain had the highest fitness in both resources, and hence, measured trait variation could have a significant impact on population processes in different habitats.

Population Persistence

Almost all populations that became extinct during the study were single-strain populations with very low founding genetic variation (fig. 1*A*; in wheat, six out of a total of seven extinct populations were single strain; in wheat + corn, four of four; in corn, 16 of 20). However, none of the highest-diversity (four-strain) populations became extinct in any habitat (five replicate populations per habitat). While genetic variation generally tended to increase population persistence in all three habitats, the interaction term between habitat and genetic variation for the proportion of extinct populations was not significant (fig. 1*A*; generalized linear model with binomial error, model $\mathrm{AIC} = 26.11$; effect of genetic variation, $P < .001$; effect of habitat, $P < .001$). Habitat-specific analyses show that the positive effect of genetic variation was statistically significant only in the corn treatment (Fisher's exact test, $P < .001$), with no significant association between genetic variation and the proportion of extinct populations in wheat ($P = .1$) and wheat + corn habitats ($P = .19$). These results indicate that genetic variation generally increased population persistence but that the effect size was greatest under strong selection.

Population Stability

Excluding extinct populations, genetically more diverse populations were more stable in both wheat and wheat + corn habitats (fig. 1*B*; table 3). Note that CV is inversely related to stability; thus, a higher CV indicates greater size fluctuations and lower stability. Habitat alone also significantly affected population CV: populations were less stable in the wheat + corn habitat than in the wheat-only habitat (fig. 1*B*; table 3).

In the wheat habitat, high-diversity populations did not have maximum stability. Single-strain populations of Pak-3, as well as some intermediate-diversity populations, were more stable, although high-diversity populations were, on average, most stable (fig. 1*B*; also see fig. 2). However, in the wheat + corn habitat, high-diversity populations founded with all four strains had the highest stability (fig. 1*B*), equivalent to their stability in wheat. Thus, while low-diversity populations responded negatively to the novel

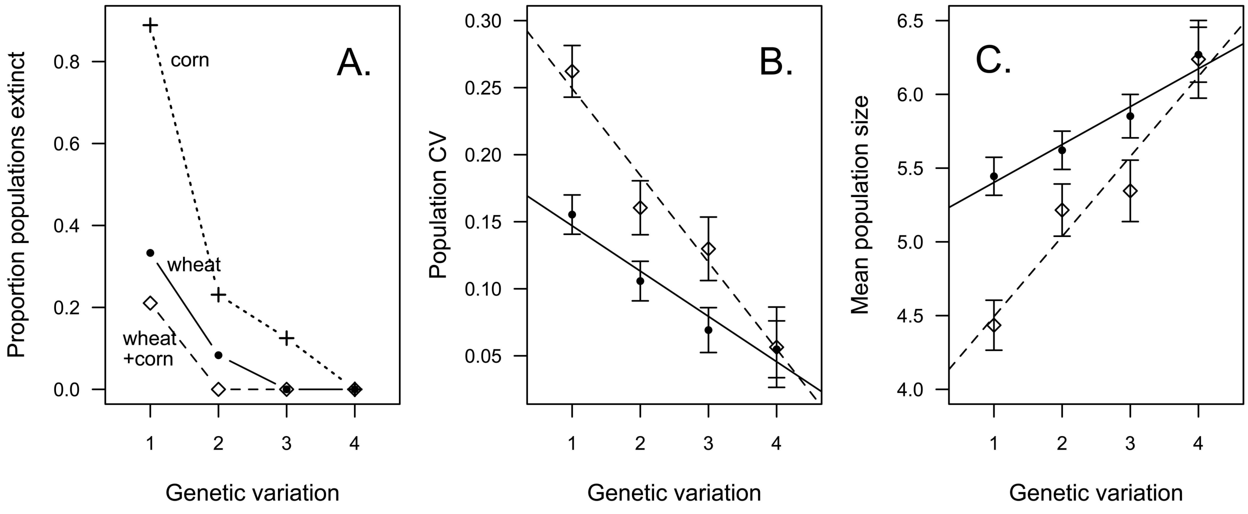

Figure 1: *A*, Proportion of extinct populations; *B*, coefficient of variation (CV) of population size; and *C*, natural log of mean population size, as a function of founding genetic variation (i.e., the number of different founding strains). Population parameters are shown for each habitat treatment: corn (*plus signs*, *dotted line*) wheat (*circles*, *solid lines*), and wheat + corn (*diamonds*, *dashed lines*). Each point is the mean of all strain combinations within a level of genetic variation. Lines in *B* and *C* are fitted least squares regression lines. Standard error bars in *B* and *C* were calculated as the average standard error for strain combinations within each level of genetic variation (see "Methods").

habitat, high-diversity populations showed a lack of response, leading to the apparent difference in the slopes of the regression lines in the two habitats (fig. 1*B*). However, this difference was not statistically significant (table 3). Hence, contrary to expectation, the effect of genetic variation on population stability was statistically indistinguishable in both habitats, although genetic diversity and habitat independently affected population stability.

Population Size

As expected, population size in the wheat-only habitat was greater than that in the novel wheat + corn habitat, which contained only half the amount of the ancestral wheat resource (fig. 1*C*). Mean population size also increased with increasing genetic variation, but there was no significant interaction effect of genetic variation and habitat on population size (table 3; fig. 1*C*). Thus, genetic variation and habitat independently affected mean population size during the study, reflecting the patterns observed for population stability.

Elucidating Mechanism: Testing for Selective Fixation of Alleles

In both wheat and wheat + corn habitats, high-diversity (four-strain) populations had greater stability and size than single-strain populations (fig. 2), indicating that the effects of genetic diversity were not additive in either habitat. Potential nonadditive mechanisms responsible for the observed increase in population size and stability of more diverse populations include (*a*) a selective sweep of alleles from a single high-fitness founding strain, (*b*) a selective sweep of a novel allele combination, (*c*) individual niche complementarity without a selective sweep, and (*d*) a combination of one or more of these mechanisms.

The selective-sweep hypothesis leads to two testable predictions. First, the size and stability of high-diversity populations would match those of single-strain populations carrying the selected allele(s). Pak-3 individuals had the highest fecundity and survivorship in wheat (table 1); hence, an a priori prediction would be that Pak-3 alleles would be selectively favored in high-diversity wheat populations. This prediction is supported by the observation that the stability and size of single-strain populations of Pak-3 were equivalent to those of four-strain high-diversity populations, whereas monocultures of the other three strains had a significantly poorer performance (fig. 2*A*; table 4). Second, we would expect that population stability and size would be positively correlated to the initial frequency of the selected allele(s). This prediction is largely borne out when population size and stability are regressed against the fraction of founding Pak-3 individuals (fig. 3*A*). Population size increased significantly with the fraction of Pak-3 individuals in the founding generation (linear regression: $R^2 = 0.22$, $t = 2.4$, $P = .026$), and a nonsignificant but positive relationship was observed between population stability and the fraction of Pak-3 individuals

Table 3: Results of analyses of population size and stability

Response variable and effect	Habitat	Estimate	SE	t	$P(>\|t\|)$
Coefficient of variation:					
Genvar	W	−.036	.005	−6.24	.025
Genvar	W+C	−.066	.010	−6.12	.026
Habitat				4.48	.011
Habitat × Genvar				−2.49	.067
Mean size:					
Genvar	W	.257	.039	6.57	.022
Genvar	W+C	.542	.107	5.06	.037
Habitat				−4.35	.012
Habitat × Genvar				2.50	.066

Note: Genvar = genetic variation; W = wheat; C = corn. Results for genetic variation are from a weighted linear regression of the response variable on genetic variation for each habitat. Results for habitat and habitat × genetic variation interaction are from *t*-tests for differences between the intercepts and slopes of regression lines in the two habitats.

($R^2 = 0.14$, $t = -1.8$, $P = .087$). A similar analysis for the other three strains shows no significant relationship between the fraction of the founding population composed of the focal strain and population size or stability ($P > .1$ in all cases). These results suggest that Pak-3 alleles were selectively favored in the wheat habitat and that this selective effect resulted in the greater average stability and size of high-diversity populations.

In the wheat + corn habitat, however, it is unlikely that Pak-3 alleles dominated the gene pool. First, all single-strain populations (including Pak-3 populations) performed significantly better in combination with other strains than by themselves (fig. 2*B*; table 4). Pak-3 individuals also had poor survivorship in corn flour (table 1), making it unlikely that a selective sweep of Pak-3 alleles could lead to the enhanced performance of high-diversity populations. Finally, the fraction of founding Pak-3 individuals had no effect on the mean population size (fig. 3; linear regression: $R^2 = 0.006$, $t = -0.34$, $P = .74$), but it was associated with decreased population stability in the wheat + corn habitat ($R^2 = 0.4$, $t = 3.68$, $P = .001$). The fraction of founding individuals from the other three strains had no effect on population size or stability ($P > .05$). Therefore, a selective sweep of Pak-3 alleles (or of those alleles from the other three strains) could not be responsible for the increased size and stability of high-diversity populations. Alternative mechanisms are discussed below.

Discussion

Genetic variation for ecologically relevant traits is ubiquitous in natural populations (Mousseau et al. 2000). Not least because of its importance in conservation biology, we need to understand the various ecological and evolutionary impacts of genetic variation (Frankham et al. 2002). This experiment aimed to quantify the effect of intraspecific genetic variation on population stability in different selective environments. Results show that the stability of single-species populations increased as a function of founding genetic variation, in both novel and ancestral habitats (fig. 1*B*). Previous work suggests that genetic variation may be critical only under stressful or novel conditions, when a rapid response to selection can enhance population persistence and adaptation (Reed et al. 2002, 2003; Wise et al. 2002; Armbruster and Reed 2005; Charmantier and Garant 2005; Kristensen et al. 2008). For instance, genetic variation in *Brassica rapa* populations enhanced performance when plants were exposed to an unplanned heat stress but had no effect under otherwise benign experimental conditions (Wise et al. 2002). Experiments with *Drosophila* populations also show that environmental variability can exacerbate inbreeding depression and reduce adaptive potential (Reed et al. 2003). On the contrary, genetic diversity and habitat did not interact to affect population stability or persistence in my experiment (although the impact of genetic variation tended to be greater in novel habitats; fig. 1), suggesting that genetic variation may be beneficial not only in novel but also in ancestral habitats. The discrepancy with previous results may be partially attributed to a larger effect size in the ancestral habitat caused by differences in experimental design. First, rather than manipulate and test for the effects of reduced genetic variation by forced inbreeding, I experimentally increased the genetic variation within populations. For populations that are already inbred, the latter design likely provides a larger range of genetic variation and, potentially, larger overall effect sizes. Second, I generated diversity by mixing strains with distinct evolutionary histories and measured among-strain phenotypic variation, rather than using neutral molecular markers that are often poor indicators of ecologically relevant trait var-

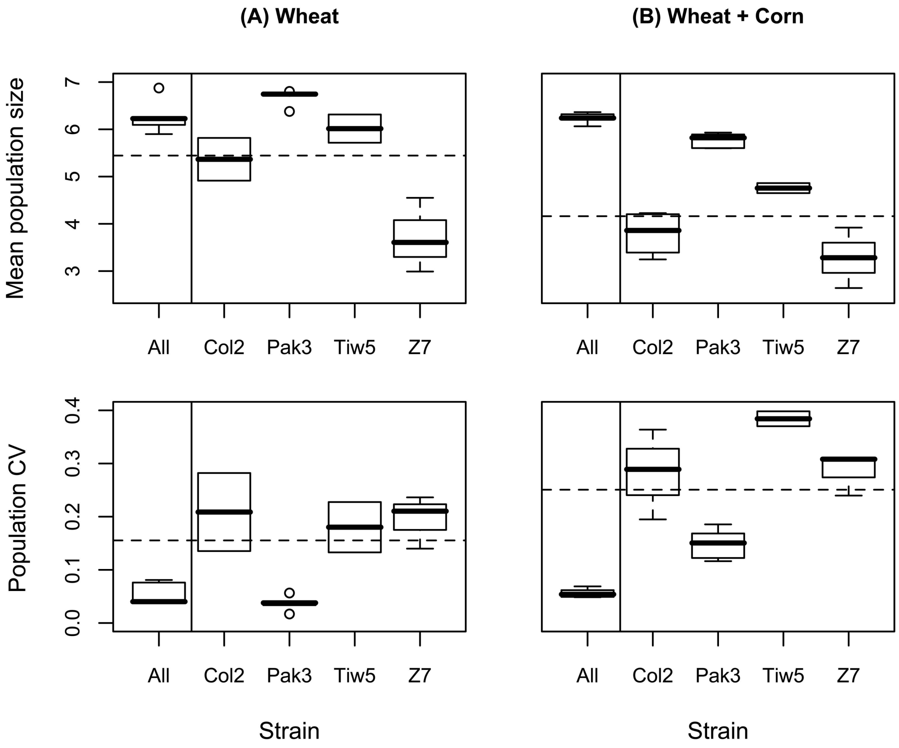

Figure 2: Box plots for mean population size and coefficient of variation (CV) of population size in two experimental habitats for single-strain (Col-2, Pak-3, Tiw-5, Z-7) and high-diversity populations composed of all four strains (All). Dashed line shows the mean value of the response variable (size or CV) for single-strain populations.

iation (see McKay and Latta 2002 for a review; for a meta-analysis, see Reed and Frankham 2001). Therefore, my experiment probably captured important ecologically relevant heritable variation, amplifying the measured effect size of such variation. Analyzing the response of various strain combinations in detail (see below) shows that the mechanism(s) responsible for the stabilizing effect of genetic variation were habitat specific.

Distinguishing Additive and Nonadditive Effects of Genetic Variation

If genetic diversity had an additive effect on population function, we would expect the size and stability of high-diversity populations to equal the weighted means of all single-strain populations (since high-diversity populations were composed of all four strains in equal proportion, this is simply their arithmetic mean). In my experiment, high-diversity populations had size and stability far greater than the single-strain overall means (fig. 2), indicating that the effects of genetic diversity were nonadditive. The selective fixation of some alleles, coexistence of different alleles as novel recombinant genotypes in high-diversity populations, or among-individual variation in niche use could be responsible for the observed positive effects of genetic diversity. Below I discuss data from both habitats (wheat only and wheat + corn) separately, to infer the causal mechanism in each case.

Nonadditive Effects in the Ancestral Habitat: Selective Sweeps

A selective sweep of beneficial alleles could be enhanced if such alleles imparted a large fitness advantage in high-diversity populations. For instance, greater productivity of clonal mixtures of the alga *Chlamydomonas reindhartii* was explained by the presence of a highly productive clone that quickly dominated the population (Bell 1991). Mating in *Tribolium castaneum* occurs rapidly and multiple times after sexual maturity (Pai and Yan 2003); hence, most adults used to initiate the experimental populations had probably already mated within their parent stock population. Thus, eggs in the experimental populations would largely carry strain-specific allele combinations, and the next generation could have a higher representation of more fecund strains, allowing their alleles to rapidly increase in

Table 4: Strain-specific response to increased genetic variation in different habitats

Response variable and strain (combination)	Wheat: Difference (strain − All)	Wheat: P (adjusted)	Wheat + corn: Difference (strain − All)	Wheat + corn: P (adjusted)
Coefficient of variation:				
Z-7 (1)	.14	.006	.23	<.001
Pak-3 (2)	−.02	.963	.09	.017
Col-2 (3)	.15	.008	.22	<.001
Tiw-5 (4)	.12	.033	.33	<.001
Mean size:				
Z-7 (1)	−2.55	<.001	−2.96	<.001
Pak-3 (2)	.41	.619	−.47	.262
Col-2 (3)	−.90	.187	−2.44	<.001
Tiw-5 (4)	−.25	.960	−1.48	.001

Note: Results of Tukey HSD pairwise contrasts are given for all single-strain and four-strain (All) populations in each habitat, along with the difference in the mean response of each single-strain and four-strain combination.

frequency. Pak-3 individuals had significantly greater fecundity and survivorship in wheat, and their single-strain population properties were equivalent to those of high-diversity populations in the wheat habitat (table 1; fig. 2*A*). Post hoc regression analysis shows that populations founded with a larger fraction of Pak-3 individuals were larger and more stable (fig. 3). Hence, it is likely that Pak-3 individuals dominated the dynamics of high-diversity populations in the wheat habitat through a selective sweep of their alleles. Note that heritable variation in any trait that confers an initial, large relative fitness advantage at the beginning of the experiment could determine the likelihood of a selective effect as well as the identity of traits under selection. For instance, if the experimental populations were initiated with juvenile stages instead of already mated adults, it is possible that competitive ability, relative survivorship, or degree of cannibalism would also determine whether and which alleles were selected. Thus, these results can probably be generalized for different organisms and experimental conditions and for varying life histories.

Nonadditive Effects in the Heterogeneous Habitat: The Role of Sexual Recombination

In the wheat + corn habitat, it is unlikely that a selective sweep of alleles from a single founding strain caused greater stability of more diverse populations. Low-fecundity founding strains that could be outcompeted by Pak-3 in wheat had a higher survival in (and behavioral acceptance of) corn flour (table 1). Thus, only half the available resource in this habitat offered a relative fitness advantage for alleles from the Pak-3 strain, making it unlikely that Pak-3 alleles could sweep to fixation. Furthermore, the negative correlation between population stability and the fraction of founding individuals from Pak-3 (fig. 3) and the lack of a correlation for the other strains support the conclusion that no single strain dominated high-diversity population dynamics in the wheat + corn habitat.

Thus, more diverse populations in the wheat + corn habitat had greater stability due to either individual niche complementarity (resource specialization) or a selective sweep of a recombinant, high-fitness genotype. An a priori hypothesis may predict that the former mechanism is likely to operate in a heterogeneous habitat such as the wheat + corn treatment, where broad resource niche diversification is possible and different alleles can coexist as a result of such diversification (Hedrick 1986). Genetic variation for resource use could lead to greater niche complementarity in more diverse populations, and increased exploitation of novel niches could in turn lead to higher population size and stability. For instance, niche complementarity enhanced the performance of sea grass populations with greater clonal diversity (Reusch et al. 2005). In sexual species, niche complementarity can be measured as the degree of individual variation in niche use (Bolnick et al. 2003). A positive correlation between niche complementarity and population size and stability would indicate that niche complementarity was responsible for increased stability of more diverse populations. However, stable carbon isotope analysis of beetles sampled from the experimental populations shows the absence of such a positive correlation (D. Agashe and D. I. Bolnick, unpublished manuscript). Therefore, unlike in clonal sea grass populations (Reusch et al. 2005), niche complementarity probably did not impart greater stability in the stressful (novel wheat + corn) environment.

A third nonadditive mechanism that could explain the greater stability of more diverse populations is a selective sweep by a recombinant genotype, which would be more likely in high-diversity populations with greater standing genetic variation. As mentioned above, stable-isotope data

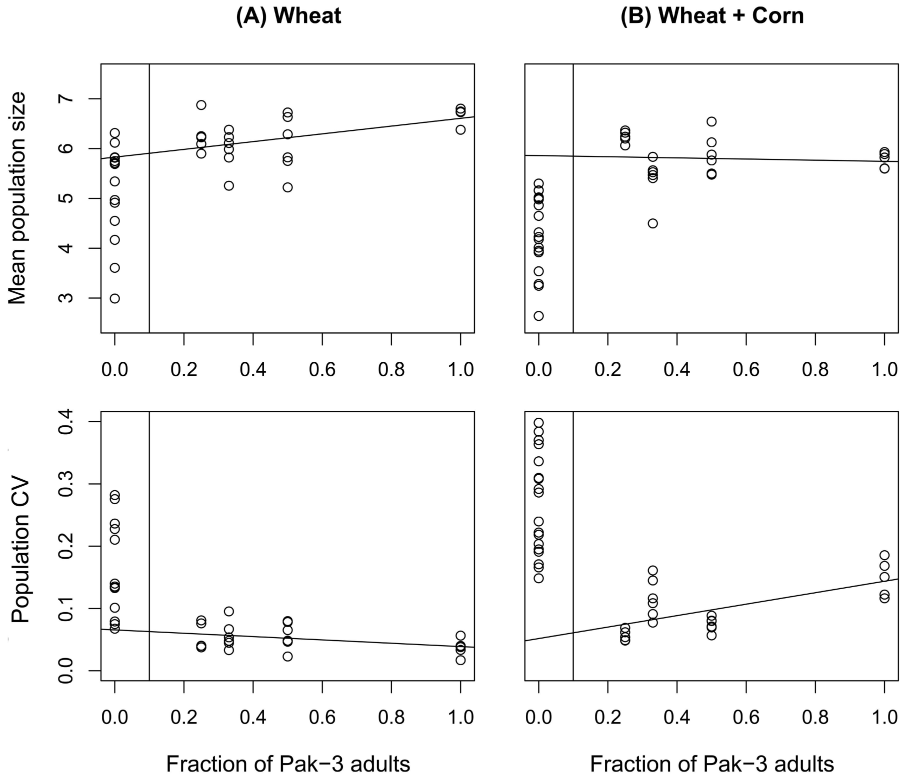

Figure 3: Effect of fraction of Pak-3 adults on coefficient of variation (CV) and mean population size, in which each point represents data for a single population. For values > 0, the X-axis also represents a decreasing level of genetic variation (e.g., a Pak-3 fraction of 0.25 indicates high-diversity all-strain populations, and a Pak-3 fraction of 1 indicates single-strain Pak-3 populations). Leftmost data points in each panel represent all populations founded without any Pak-3 individuals (fraction Pak-3 $= 0$). With these points excluded, the least-fit regression of CV and population size on the fraction of Pak-3 adults is indicated with lines.

indicate that individuals in all populations used equivalent amounts of corn flour in addition to wheat flour. Therefore, populations that maintained greater size and stability could do so only if they were more efficient in their use of one or both resources. A generalist genotype able to exploit both resources more efficiently than ancestral genotypes would have greater fitness and could increase in frequency in the population. To test this hypothesis, one would have to determine whether efficiency of wheat and corn flour use (quantified as, e.g., the number of viable offspring produced per gram of flour consumed by an individual) was positively correlated with population stability or size. I lack such data for these experimental populations; hence, the mechanism for increased population stability of diverse populations in the wheat + corn habitat remains to be explicitly tested. On the basis of the evidence presented above, however, I can reject two commonly invoked causal mechanisms: selective sweeps of alleles from founding strains and niche complementarity.

In the absence of assortative mating, sexual recombination would generate novel genotypes in each generation, in addition to breaking apart favorable allele combinations. Therefore, it is also possible that multiple recombinant genotypes led to the increased size and stability of more diverse populations. Whether or how long such genotypes coexisted or whether they outcompeted each other in rapid succession remains to be tested. In contrast, in asexual populations novel genotypes can be generated only via mutation, and the coexistence of multiple beneficial mutations is relatively rare. Compared to standing genetic variation, mutation also typically leads to lower rates of adaptation (see Barrett and Schluter 2008 for a review). Thus, in the heterogeneous habitat, sexual recombination appears to have played a major role in determining the mechanism through which intraspecific founding genetic variation affected population parameters. Because previous experiments documented nonadditive benefits of genetic diversity in clonal species (e.g., Reusch et al. 2005; Crutsinger et al. 2006), this study represents one of the few reports of a nonadditive mechanism arising from sexual recombination.

Ideally, a selective effect should be tested using the relative abundance of functionally important strain-specific alleles in the experimental populations. However, this was difficult because of the paucity of knowledge of specific loci associated with life-history traits in *Tribolium*. While many studies use neutral molecular markers to measure quantitative trait variation, the lack of concordance between the two is well established (Reed and Frankham 2001; McKay and Latta 2002); in addition, sexual recombination can rapidly dissociate correlations between neutral markers and positively selected alleles. Hence, using molecular markers would not be informative in this experiment. Consequently, the stabilizing effect of genetic variation demonstrated here refers specifically to founding genetic variation.

It is important to note that the mechanisms for the effects of genetic variation discussed above need not be mutually exclusive. For example, selection for high fecundity on wheat could initially increase the frequency of Pak-3 alleles in wheat + corn populations, since egg-to-adult development time is longer in corn flour (D. Agashe, unpublished data) and survivorship is lower (table 1). As population size increased and wheat became a limiting resource, niche variation could maintain different alleles in the population. Here I lacked the ability to explicitly test for such combined or sequential effects, but it is possible to do so with long-term measurement of temporal changes in the relative abundance of functional alleles, coupled with measures of temporal change in individual variation in niche use efficiency. Such studies will be feasible in the future, when cost-effective molecular resources, including knowledge of specific loci tightly linked to functional fitness traits under selection, are developed for more species.

The beetle strains used in my experiment likely suffered from inbreeding depression during ~20 years of laboratory maintenance. Thus, the results presented above could also be interpreted as evidence that outbreeding (in populations founded with more than one strain) increases population stability by increasing mean fitness due to heterosis. However, the benefits of outbreeding depend on the population history and the selective environment, on measured traits and their genetic architecture, and on the risk of outbreeding depression (see Edmands 2007 for a recent review; for lineage effects in *T. castaneum*, see Hohenboken et al. 1991; Pray and Goodnight 1995). In my experiment, outbreeding was detrimental for Pak-3 inbred populations but beneficial for the other strains (table 4). Furthermore, high individual fitness does not always translate into population performance (e.g., strain Tiw-5 had high individual fitness but low population persistence in wheat; table 1; fig. A1). Under soft selection, for example, population growth is governed by frequency- and density-dependent interactions among individuals (Wallace 1975). The mechanism(s) responsible for population-level effects of inbreeding rescue and increased genetic variation (discussed above) may thus be similar and, consequently, difficult to distinguish. Inbreeding rescue may have contributed to the stability of more diverse populations, but lineage effects, high fecundity, and the inherent density-dependent dynamics render it an incomplete explanation.

Genetic Variation and Population Extinction

Numerous studies have shown that the probability of population extinction increases as a function of inbreeding or loss of genetic variation (Frankham 1995; Willi et al. 2006). Results from my experiment corroborate these results, showing that population extinction is a decreasing function of founding genetic variation (fig. 1*A*). Relatively few studies have examined the impact of ecologically relevant genetic variation on population persistence in different habitats, although mathematical models indicate that the benefits of genetic variation are greater in more variable environments (Lande and Shannon 1996). Although my experiment does not directly test this theoretical prediction, the data indicate the lack of a genetic variation by habitat interaction on population extinction. Ecologically relevant genetic variation may thus prevent population extinction in diverse habitats and under different degrees of environmental stress and may be more widely beneficial than previously believed.

Conclusions

Recent literature has emphasized the close connection between ecological and evolutionary dynamics via feedback and the pressing need for studies that examine the mechanistic basis of such concurrent dynamics (Hairston et al. 2005; Carroll et al. 2007; Fussmann et al. 2007; Ives and Carpenter 2007). As a step in this direction, I show here that an "evolutionary" parameter (genetic variation) can greatly alter critical "ecological" characteristics (population stability and persistence) and that the mechanisms causing this effect are habitat dependent. The latter observation also suggests that heritable variation, which is important for subsequent evolution, may in turn be maintained in the long term because of greater population stability in novel heterogeneous habitats. Further experiments are required to specifically test this hypothesis and establish the mechanism(s) responsible for the outcome.

While this study shows that the dynamics and persistence of a density-regulated pest species are positively affected by intraspecific genetic variation, studies on other organisms under different selective environments are needed to evaluate the impacts of genetic diversity in a broader context. Particularly important are studies with natural populations, which typically harbor more genetic variation than laboratory populations and may thus show effect sizes larger than those measured in this experiment. However, natural populations are also subject to a number of simultaneous environmental and interspecific stresses, as well as gene flow via migration, and it is unclear how these factors will affect the impact of genetic variation on population stability. Because the speed and outcome of evolutionary change may differ greatly among sexual and asexual species, we need long-term studies on the community and ecosystem effects of intraspecific diversity, specifically in sexual species.

Changes in intraspecific as well as interspecific diversity are common in natural populations and are associated with various events such as colonization, range expansion, and extinction of species. In addition, there is increasing interest in the form, mechanistic basis, and generality of the relationship between intra- and interspecific diversity (Vellend and Geber 2005; Vellend 2008). Hence, measuring the impact of changes in intraspecific genetic variation for population dynamics has far-reaching implications for our understanding of the generation and maintenance of biodiversity.

Acknowledgments

I thank C. Paciorek for statistical advice; D. Bolnick, K. Kunte, M. Leibold, S. Pawar, and two anonymous reviewers for discussion or comments on the manuscript; and G. Calabrese, J. Conover, and J. Falk for invaluable laboratory assistance. This work was supported by research fellowships from the Graduate Program in Ecology, Evolution, and Behavior at the University of Texas, Austin.

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