

Mechanisms that Drive Evolutionary Change

INSIGHTS FROM SPECIES INTRODUCTIONS AND INVASIONS

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One way to summarize the evolutionary dynamics of species introductions is to estimate how levels of genetic diversity in non-native populations are different from those of their source populations. While it is typically assumed that a significant loss of diversity will be associated with species introductions, the actual effect may be more complex, depending on propagule pressure and patterns of diversity and population structure in the native range of a species. We review a number of studies of animal species introductions in which allelic diversity and heterozygosity in the non-native and source ranges of each species can be compared, and find that the typical loss of diversity is minimal. The generality of this pattern may provide new insight into debates over the prevalence of stochastic processes in generating novel phenotypes or coadapted gene complexes in founder populations. These results suggest that the response of founder populations to natural selection in a novel environment is generally more important than the stochastic effects of the founder event itself in determining the evolutionary trajectory of a population.

Introduction

In 1880, local fishermen introduced grayling (*Thymallus thymallus*) into Lake Lesjaskogsvatn in Norway. Subsequent introductions and dispersal of this fish into nearby lakes provided an exceptional window into the phenotypic and genetic changes that occurred as grayling populations became established in novel environments. After fewer than 25 generations of isolation, levels of among-population variance for seven heritable life history traits (such as yolk sac volume and growth rate) were consistently higher than levels at microsatellite (presumably neutral) loci (Koskinen et al. 2002). Despite the fact that a small number of fish initiated each population, the loss of genetic variation due to founder effects, population bottlenecks, and random genetic drift (see Box 9.1 for definitions of key terms and concepts used in this chapter) apparently had little effect on the overall phenotypic divergence of these populations. Instead, the observed shifts in life history traits were largely attributable to natural selection (Koskinen et al. 2002). This example is consistent, therefore, with the view that introductions and invasions frequently involve episodes of rapid evolution (reviewed in Reznick and Ghalambor 2001; Sakai et al. 2001; Lee 2002). It also embodies one of the most fundamental debates in evolutionary biology; namely, the relative importance of deterministic processes such as natural selection versus stochastic processes such as genetic drift as causes of evolutionary change (reviewed in Reznick and Ghalambor 2001; Dupont et al. 2003).

Ever since the classic debate between Fisher (1930) and Wright (1932), one of the major challenges facing evolutionary biologists has been to understand how selection and drift, along with additive and higher-order interactions (e.g., dominance and epistasis) among genes, contribute to evolution in natural populations (Coyne et al. 1997; Wade and Goodnight 1998; reviewed in Brodie 2000). The Fisherian paradigm holds that natural selection generally drives evolutionary change within populations, giving primacy to the role of mass selection acting on additive genetic variance produced by the small, independent contributions of numerous loci to fitness. In contrast, Sewall Wright emphasized the importance of random genetic drift in population differentiation. Specifically, his shifting balance theory conceived of an “adaptive landscape” that described the relationship between the summed effects of interactions between the environment and additive genetic variance, as well as higher-order epistatic interactions among genes, on fitness (Wright 1932). Whereas selection acted to drive a population toward any of the fitness peaks on the landscape, drift explained how populations crossed valleys of low fitness separating adaptive peaks (Figure 9.1). Thus, Wright (1932) emphasized that stochastic processes, in concert with higher-order epistatic interactions among alleles at different loci, could constrain mass selection, especially in small, subdivided populations.

To what extent do founder effects or population bottlenecks, genetic drift, and higher-order genetic interactions influence the outcomes of Fisherian mass selection, particularly when populations experience novel selective regimes? Progress toward answering this fundamental question requires, first, docu-

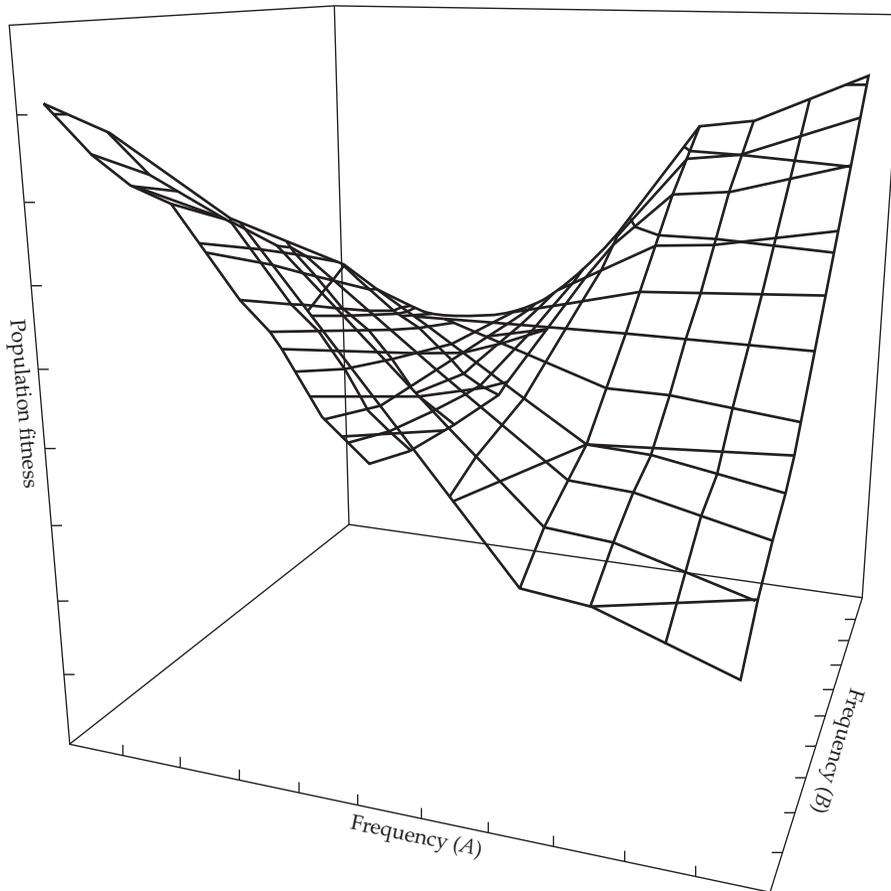


Figure 9.1 Adaptive landscape model. Developed by Wright (1932), this model is intended to portray the interactions of genes and their effect on fitness. While it is typically represented as a simple model balancing the effects of two loci (here the frequency of an allele at locus *A* and an allele at locus *B*), the interactions across an entire genome are of course more complex. The question is how populations move from one phenotypic optimum to another, given that this requires passing through genotypic combinations that are maladaptive (the “valleys”). While proponents of mass selection (*sensu* Fisher 1931) argue that most evolutionary adaptation is the result of natural selection acting on mutations, recombination events, and gene interactions, Wright (1932) proposed that genetic drift in smaller populations—which may stochastically push populations toward suboptimal genotypic combinations— aids the process of moving from one peak to another. The debate over the generality of these models for evolution is a fundamental and persistent issue (Skipper 2002).

menting genetic and phenotypic responses of natural populations to changes in selective regimes, and second, determining the contributions of additive, dominance, and epistatic variance to fitness (see papers in Wolf et al. 2000). Because it is often possible to infer divergence times from source populations,

BOX 9.1 Key Terms and Concepts

Here we discuss a few terms that are necessary for biologists to critically evaluate genetic characterizations of species introductions and the potential for evolution following these events. Demonstrating whether populations have evolved following a species introduction typically involves characterizing whether the mean phenotype of individuals has shifted, and whether it has shifted in a heritable way. A **trait** or set of traits may be measured to determine how much variance there is for a phenotypic character, whether the trait is structural, behavioral, or ecological. The variation in this phenotypic trait is determined by the level of **genetic variation** (V_G) at related loci, the plastic response of an individual to the environment, and the interaction between particular genotypes and environmental variables.

The genetic variation that contributes to a heritable trait may be separated into three primary components. **Additive genetic variance** (V_A) involves the whole-genome allelic diversity that contributes to phenotypic variation and is considered the most direct target for natural selection. If the contribution of a locus is additive, then each allele contributes a fixed value to the measure of a quantitative trait; higher-order interactions modify this contribution, and thus do not contribute additively to the phenotype. For example, genetic variance due to **dominance** (V_{A_d}) arises because of interactions among alleles at the same locus, such that the expression of one may mask the expression of the other, and may be important following a **population bottleneck** (the short-term restriction in population size associated with species introductions) because the frequency of particular dominant/recessive allelic combinations may change dramatically. Variance due to **epistasis** (V_{A_B}) is caused by the interactions among

genes. It is thought by some to be particularly important during and after genetic bottlenecks because particular gene complexes may be altered dramatically by the loss of alleles at particular loci.

A bottleneck in terms of allelic diversity and **heterozygosity** (a measure of allelic diversity within as well as between individuals in a population) arises because a species introduction involves taking a sample from the original source population. If this sample is large, it is likely to represent the whole of source population diversity, but as the sample size of the introduced population shrinks, it is more likely that rare alleles will be omitted. Further, because of strong inbreeding among individuals in the founder population, there will be transient linkage disequilibrium between loci (genes that are not physically linked in the genome may be associated with each other because of the small number of gametes that are involved in the founding of a population) that may temporarily change the evolutionary dynamics of the population.

What is frequently debated by evolutionary biologists is the importance of these transient **founder effects**. For example, rare alleles may be lost or overrepresented in the introduced population. If these alleles are **selectively neutral**, it is of no consequence for the fitness or phenotype of the individuals, but if the alleles are rare in the source population, either because they are deleterious (that is, they potentially reduce the fitness of individuals) or because they are maintained by frequency-dependent selection, then the resulting evolutionary change could be more dramatic and long-lasting. For the same reason, the contribution of dominance interactions to genetic variance following a bottleneck is extremely variable (Barton and Turelli

BOX 9.1 (continued)

2004), outweighing much of the contribution of interactions among loci.

The often-discussed “**conversion**” of epistatic genetic variance to additive genetic variance involves changes in the background of allelic diversity at interacting loci; the loss of diversity at one locus may allow greater expression of the allelic diversity at another locus, contributing to additive variation and exposing this variation to natural selection (Brodie 2000). For example, gene interactions may include variation at distinct loci with balancing effects on fitness (e.g., for two loci *A* and *B*, each with two alleles, where selection favors the A_1B_2 and A_2B_1 genotypes over the A_1B_1 and A_2B_2 genotypes), and the expression of additive genetic variation may increase following a population bottleneck (e.g., the loss of A_1 due to a founder effect will result in the expression of the *B* alleles with no compensatory interactions—the A_2B_1 genotype should still be favored over the A_2B_2 genotype in this case, and the epistatic variance caused by interactions between these two loci is then converted into the additive effect on fitness of the *B* locus alone).

The strength of a bottleneck may be measured by the proportional loss (*F*) of **heterozygosity** at a number of presumably **neutral markers** (those that are believed to be unimportant for fitness, such as silent mutations that do not change the amino acid sequence of a protein) or by the loss of allelic diversity itself. The proportion of additive genetic variance that may be gained through epistatic interactions, following a bottleneck, is on the order of F^k (where *k* is the number of interacting loci; Barton and Turelli 2004). Because the contribution of epistatic interactions to phenotypic variance only declines as a function of $(1 - F^k)$, and the amount of additive genetic vari-

ance that makes it through a bottleneck is $(1 - F)$, epistatic and dominance interactions can contribute relatively more to phenotypic variance after a severe bottleneck.

The effects of population bottlenecks are inherently linked to the concept of **effective population size** (N_e), a value that suggests the average number of individuals in a population that contribute genetically toward the following generation. This parameter, which reflects the life history and demography of a population or species, may be measured using both temporal changes in allele frequencies (e.g., Waples 1989) as well as the statistical distribution of nucleotide substitutions in a population (Nei 1987). The ratio of N_e to the actual census size depends on a number of factors (Turner et al. 2002). Historical bottlenecks will reduce the measure of inbreeding effective population size (a geometric mean of the number of successfully reproducing individuals over time), and high variances in reproductive success will also lower N_e of a population. The strength of **random genetic drift**, or the stochastic variation in allele frequencies from one generation to the next, is inversely proportional to N_e ; small isolated populations are subject to stronger effects of drift.

When a species' source region contains several demographically isolated populations (**population genetic structure**), the introduction of that species involves a sample from at least one—and maybe several—genetically distinct lineages. Depending on the time inferred from the phylogeny, admixture of populations in the introduced region may involve closely related populations or distinct species. **Admixture** refers to the demographic linkage of two or more historically isolated lineages in the same introduced range, and may or may not involve **hybridization**, the successful

BOX 9.1 *(continued)*

mating between members of different lineages. Hybridization allows genetic interactions between two isolated populations to occur; this may involve both dominance and epistatic interactions that affect the fitness of the hybrid individuals (Willett and Burton 2003).

Introgression occurs only if hybrid individu-

als are successful in reproducing with individuals from one or both of the original lineages (Stewart et al. 2003). Methods of assessing deviations in allele frequencies from Hardy-Weinberg equilibrium provide some insight into the degree to which introgression has occurred (Anderson and Thompson 2002).

and in some cases to reconstruct directly the geographic, demographic, and ecological history of an introduction or invasion, genetic studies of introduced and invasive species can often provide unusually detailed, and sometimes replicated, chronicles of evolutionary change (Le Page et al. 2000). Moreover, to the extent that introductions and invasions involve rapid evolution, it is often possible to observe directly associated genetic and phenotypic changes. Biological introductions therefore represent potentially powerful—albeit often undesirable—experiments that may improve our understanding of how stochastic and deterministic forces shape evolutionary change.

There is little question that the strength and direction of natural selection can change rapidly during the course of an invasion (reviewed in Sakai et al. 2001; Lee 2002). It is also clear that many of the source populations for introductions and invasions possess ample additive genetic variance and may therefore endow introduced populations with the genetic variation necessary to respond to selection (e.g., Huey et al. 2000). On the other hand, if relatively few individuals found an introduced population, and the population therefore experiences an extended bottleneck before establishment and expansion, then the loss of allelic diversity and additive genetic variance could seriously limit the potential for rapid evolutionary change (reviewed in Willis and Orr 1993; but see Whitlock 1995; Whitlock and Fowler 1999). Founder effects and drift may also lead to the “conversion” of epistatic (e.g., Goodnight 1988; Cheverud 2000) and dominance (e.g., Willis and Orr 1993) variance for fitness into additive genetic variance. This conversion could subsequently fuel evolutionary change during an invasion (Reznick and Ghalambor 2001; Lee 2002). Thus, in theory, both natural selection and stochastic processes could cause (or inhibit) evolutionary change over the course of an invasion: newly founded populations could experience a loss or gain of additive genetic variance, an increase or decrease in the importance of epistatic and dominance interactions, and an enhanced or diminished response to selection.

In this chapter, we analyze patterns of genetic change that accompany introductions and invasions, emphasizing the general insights that such patterns (or their absence) provide into the roles of stochastic and deterministic processes

as agents of evolutionary change. We begin by discussing the importance of genetically characterizing the full spectrum of populations that represent potential sources for introductions. We then assess the strengths and limitations of several genetic approaches widely used to identify source populations and to reconstruct the demographic history of invasion, a step that is easy to discount but critically important to our ability to make inferences of ecological and evolutionary change in introduced species. Those familiar with these methodological issues should skip to the next section, "Predicted Changes in Genetic Diversity during Introductions," in which we summarize some of the relevant theory and survey genetic studies of introduced (primarily animal) species to evaluate the contributions that drift, selection, mutation, and higher-order genetic interactions make to observed changes. The final section of the chapter evaluates the types of evolutionary forces that are likely to dominate the evolution of new phenotypes in introduced populations. (See Novak and Mack, this volume, for a comparable analysis that emphasizes plants.)

Establishing the Baseline for Evolutionary Changes

The process of establishing the evolutionary "baseline" for an introduction or invasion, as we define it here, has three key components. The first is to identify the source population(s) of an introduction. The second is to identify the genetic characteristics of that source with respect to selectively neutral markers as well as heritable traits that may be under selection. The third is to characterize the demographic history of introduction, establishment, and spread, as this history provides critical information on the size of an introduced population and hence provides critical clues to the potential action of different evolutionary forces. We emphasize the analysis of neutral markers in this section partly because such markers most accurately reflect a population's demographic history (Avice 2000). However, the genetic markers used to identify source populations and characterize the demography of introductions and invasions are unavoidably not those of greatest interest in terms of evolutionary responses of introduced species. Unfortunately, there are just a handful of studies, which we discuss later in this chapter, that characterize baseline conditions for heritable traits that are potentially subject to selection.

Identifying the source population(s)

The assertion that biological introductions and invasions often entail evolutionary change comes from observations of introduced or invasive populations exhibiting altered ecological interactions, behaviors, or phenotypes relative to source (or other introduced) populations (Sakai et al. 2001). Thus, identifying the source population(s) of an introduction reduces the potential for making false inferences about the nature and magnitude of evolutionary changes during introductions and invasions (Kolbe et al. 2004). For instance, observed

divergence among introduced populations may reflect extant differences among source populations, rather than post-introduction evolution (Lee 1999). From a practical perspective, identification of the correct source population(s) for an introduction can also simplify the development of effective biological control (Bartlett et al. 2002; Roderick and Navajas 2003; Baliraine et al. 2004).

There are in effect two steps to identifying the source population(s) for an introduction or invasion. The first is to characterize the geographic region that encompasses potential source populations and to distinguish those sources from regions or populations that represent introductions; the second involves reconstructing the history of introductions and identifying the source populations that gave rise to those introductions. Ecological data, including historical descriptions of a species' range and potential range extensions, typically are the starting point for circumscribing the native range of an introduced species and for characterizing phenotypic attributes that may be related to evolutionary changes associated with the introduction. For example, historical observations show that the brown anole (*Anolis sagrei*) is native to Caribbean islands, although populations have now been introduced worldwide (Kolbe et al. 2004). However, the historical data fail to reveal the pathways by which *A. sagrei* spread beyond the Caribbean and the evolutionary changes that occurred as the species' range expanded.

Genetic information provides an approach that is complementary to ecological and historical data for distinguishing source populations, establishing baseline conditions, identifying introduced populations, and characterizing evolutionarily important changes in the genetic composition and population characteristics (such as size and connectivity) of species during the stages of introduction, establishment, and spread (Hebert and Cristescu 2002). The first component of a genetic approach to identifying the source population(s) of an introduction involves surveying multiple populations across the entire native range for variation at molecular markers. If populations in the native range are genetically homogeneous, then it will be difficult to narrow the search for a source population. In contrast, if the native region contains genetically diverse populations—as in *A. sagrei* (Kolbe et al. 2004)—and these populations exhibit significant population genetic structure, then it may be possible to identify the source population(s) most likely to have contributed to an introduction. Once the native region has been surveyed, the same molecular markers can be used in the introduced populations to help characterize (1) their sources, (2) the evolutionarily relevant demography of the species introduction, including the number of founder individuals and the frequency and timing of subsequent introductions from multiple source populations, and (3) the genetic changes that accompanied the introduction.

Genetic methods for identifying sources

There are two basic methods of obtaining some, or all, of this genetic information. One method combines genealogical and geographic information in a

phylogeographic framework to reconstruct the history of introductions and invasions (Avisé 2000); the other uses comparisons of allele frequencies across populations to determine the likelihood that a particular introduced population originated from an array of potential sources (see Davies et al. 1999, and Roderick and Navajas 2003 for reviews). In this section, we briefly assess the strengths and weaknesses of both of these approaches.

Phylogeographic methods establish the genealogical relationships of individuals from throughout a species' distribution. Much of this work is grounded in coalescent theory (Kingman 1982; Hudson 1990), which highlights the inherent link between the distribution of genetic variation in a population and the demographic history of that population. Greater genetic diversity is attributable to greater effective population size (N_e), and as a population grows or shrinks, or splits into smaller ones, the genetic diversity in each area reflects these demographic and distributional changes. The genetic data (such as DNA sequence data) collected for these analyses are statistically analyzed with respect to the distribution of variation within and among populations to determine whether a species' range consists of a single homogeneous set of populations linked by migration and gene flow, or whether there is significant genetic structure among populations, indicating that they have been evolutionarily and demographically isolated from one another (see Grosberg and Cunningham 2001; Roderick and Navajas 2003). The outcome is a portrait of a species' history that integrates geography with information about the shared ancestry of alleles (Beerli and Felsenstein 1999) and inferred aspects of the species' demographic history, such as effective population size and connectivity, that can strongly influence a population's evolutionary response to selection (Avisé 2000; Pascual et al. 2001; Bohonak et al. 2001). Consequently, a phylogeographic analysis can be used not only to identify source locations for introduced species, but also to reconstruct the timing and mechanisms of introduction.

The second genetic approach for identifying an introduction's source population(s) uses information about allele frequencies throughout some or all of a species' range to assign an individual, based on its multilocus genotype, to the population from which it has the highest probability of origin (Paetkau et al. 1995; Davies et al. 1999; Hansen et al. 2001; Guinand et al. 2002). Methods based on allele frequencies are especially powerful for deciphering complex patterns of admixture among populations, as when multiple genetically differentiated source populations contribute propagules to an invasive population. A principal strength of frequency-based approaches lies in their use of a large number of unlinked loci to reconstruct complex introduction and invasion scenarios. In particular, estimates of genetic parameters such as effective population size, average heterozygosity, and allelic diversity based on multiple loci usually have lower variances than estimates based on sequences from one or a few loci (Wakeley and Hey 1997). Moreover, these methods are particularly useful when different classes of molecular markers are used in tandem. For example, Estoup et al. (2001) used rapidly evolving microsatellite

markers together with more slowly evolving allozyme markers to characterize the duration and intensity of population bottlenecks in introduced *Bufo marinus* (cane toad) populations.

The power of allele frequency-based tests depends on the degree of genetic differentiation among potential source populations, the number of potential source populations, polymorphism at each locus, and the number of loci analyzed (Hansen et al. 2001; Guinand et al. 2002). Moreover, as Estoup et al. (2001) emphasized, evolutionary inferences derived from frequency-based methods are constrained by our limited understanding of how variation in many widely used markers, such as microsatellites and other fragment length polymorphisms, evolves. It is therefore difficult to specify how alleles of different sizes are genealogically related to one another. In contrast, the phylogeographic approach, directly based on DNA sequences, can incorporate more realistic models of molecular evolution. This approach can reconstruct the genealogical relationships between different sequences (and the individuals that carry those sequences). However, it is typically more expensive to obtain sequence data at even a single locus and more challenging to find variable sequence-based markers. Consequently, only one or a few loci are sequenced in most studies, seriously limiting the power of many phylogeographic studies to discriminate among invasion scenarios, especially with respect to characteristics such as admixture, the magnitude of bottlenecks, and rates of post-introduction population expansion; these limitations arise because any single gene genealogy can vary substantially from the actual evolutionary history of the introduction and invasion. If there have been multiple introductions through time so that introduced populations consist of a mixture of different sources, and/or population demography varies in space and time, then more loci will provide a more accurate and comprehensive portrait of the evolutionary dynamics of an introduction and invasion.

Recently, coalescent-based admixture methods have been developed to account explicitly for the information provided by multilocus, sequence-based genotypes. These new methods incorporate the genetic divergence between alleles into the reconstruction, rather than relying simply on allele frequencies or population summary statistics (e.g., Bertorelle and Excoffier 1998; Chikhi et al. 2001; Anderson et al. 2002). Some of these methods incorporate effects of sampling error, genetic drift, uncertainty regarding estimates of allele frequencies in source populations, and variable population sizes (Chikhi et al. 2001). These approaches appear to outperform frequency-based methods (Choisy et al. 2004). Thus, although there are still formidable empirical and economic obstacles to obtaining the necessary sequence data at multiple loci for a sufficiently large sample to estimate allele frequencies with any measure of precision, models suggest that such efforts will be necessary for reconstructing the evolutionary history of all but the simplest patterns of species introductions.

Predicted Changes in Genetic Diversity during Introductions

In this section, we briefly review some of the basic theoretical foundations for our expectations of how the genetic diversity of introduced populations should vary, primarily with respect to heterozygosity and allelic diversity. To the extent possible, we use direct genetic evidence to examine these predictions; however, in some cases in which genetic changes cannot be explicitly measured, we use presumably correlated phenotypic effects. We first explore how the population bottlenecks that are often assumed to typify the first stages of introductions and invasions should affect heterozygosity and allelic diversity. We also consider the effects of mutation and hybridization, two mechanisms that can increase components of genetic variance. Finally, we survey the available genetic data that compare source and introduced populations to determine generally how, or if, introductions affect the genetic composition of populations. As with the characterization of source populations and genetic baselines, we emphasize the changes revealed by neutral genetic markers, because data from neutral markers more directly reflect the demographic and historical elements of a species introduction, with minimal intrusion of signals due to selection. Once again, however, this emphasis is also partly due to our relative ignorance in most introduced species about changes at loci that directly influence fitness traits. Such changes will, of course, often present very different patterns of diversity and divergence among populations (Luikart et al. 2003).

Effects of population bottlenecks and drift

The prediction that stochastic processes—notably founder effects, population bottlenecks, and genetic drift—should have major effects on evolution during introductions and invasions stems from expected changes in population demography associated with the introduction, establishment, and spread of an introduced species (reviewed by Sakai et al. 2001). Introductions typically begin with a small number of propagules derived from a much larger native source population. Compared with its source population, an introduced population should have (1) lower allelic diversity; (2) lower heterozygosity; (3) different allele frequencies due to sampling effects; and (4) lower additive genetic variance. The final prediction remains the most controversial because of the potential contribution of interactions among alleles (dominance effects) and among genes (epistatic effects) to overall genetic variance (see discussion below).

The magnitude of each of these potential effects depends strongly on the extent and duration of a population bottleneck, the rate of population expansion following introduction, and levels of ongoing migration from source populations and other invasive populations (Nei et al. 1975; Austerlitz et al. 1997; Ellstrand and Schierenbeck 2000). For example, a bottleneck of short duration may not lead to a significant loss of genetic variation (Nei et al. 1975); however, even if a population's census size rebounds quickly, N_e may still be suppressed relative to expectations at demographic and evolutionary equilibrium (Gros-

berg and Cunningham 2001), since N_e is largely determined by the minimum historical census size. Therefore, the relative strength of selection (directly proportional to N_e) and drift (inversely proportional to N_e) will change during the different stages of a species introduction.

Effects of mutation

The fundamental obstacle to characterizing the importance of mutation to evolutionary changes during introductions and invasions is detection. Novel alleles sampled in invasive populations may represent *in situ* mutations; however, limited genetic sampling of a source population may not provide a comprehensive picture of the genetic diversity present in the source region (Ewens 1972). It may be difficult, therefore, to determine whether “novel” alleles in expanding, invasive populations represent *in situ* mutations or whether they were simply rare and undetected in the source population (Demelo and Hebert 1994; Bastrop et al. 1998; Wares et al. 2002). Because detection becomes much simpler when full genetic characterization of source populations can be carried out, much of our understanding of how mutation contributes to the genetic and phenotypic variation of invasive populations comes from agricultural and laboratory experiments rather than natural populations (see Keightley and Lynch 2003).

Most mutations reduce fitness and should therefore be purged from populations over time (Barton 1989; Willis and Orr 1993; Keightley and Lynch 2003). However, one key difference regarding the fate of mutations—even slightly deleterious ones—distinguishes growing populations from stationary ones: new mutations have a much better chance of becoming established in rapidly expanding populations (such as invasive populations following a bottleneck) than in populations at demographic equilibrium (Carson 1968; Nei et al. 1975; Maruyama and Fuerst 1984; Otto and Whitlock 1997). Thus, mutations should more often contribute to the evolution of invasive and other growing populations than to that of populations at equilibrium. Empirical studies, however, find that mutations often represent a negligible component of the allelic diversity present in founder populations (Bohonak et al. 2001; Estoup et al. 2001; Knowles 2004). Nevertheless, novel mutations at loci under negative frequency-dependent selection, or those that are favored under unusual or unpredictable circumstances, have a higher likelihood of becoming established in rapidly expanding populations, and could therefore play a disproportionately large role in the evolution of invasive species.

Effects of admixture and hybridization

Introductions can bring into contact previously geographically isolated and genetically differentiated taxa that can hybridize. The extent of hybridization following an introduction may span a range of potential interactions, from matings between conspecific individuals from distinct source populations (admixture of multiple introductions) to hybridization between introduced and native

species. Hybridization may be limited to the production of F_1 (first-generation) crosses, with little genetic exchange between the parental taxa. However, if hybrids can reproduce successfully with either of the parental taxa, there may be extensive introgression and, ultimately, the homogenization of genetic (and ecological) differences that distinguish the parental taxa. At the same time, introgression can bring novel genes into both the introduced and resident populations, increasing their potential for responding to selection, either through increased additive genetic variance or novel epistatic interactions.

Successful mating between previously isolated taxa can directly increase levels of additive genetic variance in hybrid progeny (Ellstrand and Schierenbeck 2000; Ayres et al. 1999). However, hybridization—especially between distantly related taxa—usually produces offspring with lower fitness relative to the fitness of parental taxa (see Arnold 1997; Willett and Burton 2003). The interactions between alleles and distinct loci that are brought together through hybridization (as with sexual recombination) accelerate the evolutionary process in these populations—some good combinations will thrive, and bad combinations will often be fatal or otherwise deleterious. However, hybridization and the subsequent influence of additive and higher-order interactions can sometimes produce offspring whose range of phenotypes transgresses that observed in the parental taxa (Arnold 1997; Ellstrand and Schierenbeck 2000; Rieseberg et al. 2003). Such transgressive phenotypes may have higher fitness than either of the parental taxa, especially in disturbed or novel environments. In this way, post-introduction hybridization among conspecific or heterospecific populations may be a primary source of rapid genetic and phenotypic change in non-native populations (e.g., Ayres et al. 1999).

Observed Effects of Introductions on Genetic Variation

The preceding sections imply that the genetic changes that accompany species introductions strongly depend on the magnitude and duration of founder effects and population bottlenecks. Neither of these variables is easy to measure directly in nature. Consequently, estimates of heterozygosity and allelic diversity, based on presumably neutral markers, are often used as proxies for how a species' evolutionary potential has been altered by a founder event.

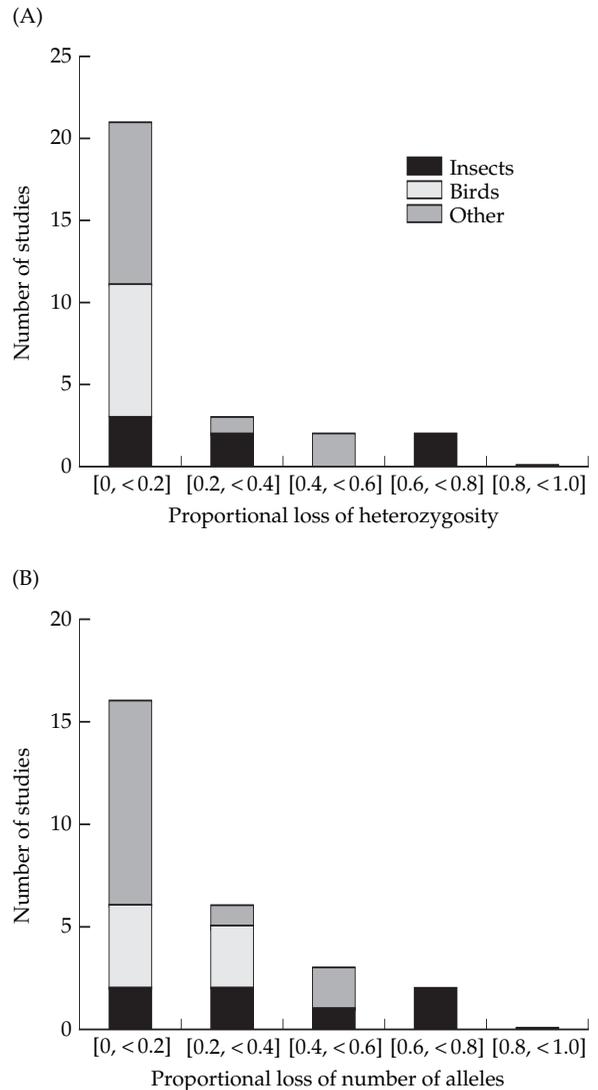
In an extensive survey of the literature on the genetic characteristics of introductions and invasions, we found 29 recent studies on animals in which relevant characteristics such as the heterozygosity and allelic diversity of source and introduced populations could be compared (Figure 9.2, Table 9.1; for a discussion of plant introductions, see Novak and Mack, this volume). These comparisons revealed that the loss of heterozygosity is typically rather small (Figure 9.2A). On average, the proportional reduction in heterozygosity ($F = 1 - H_i/H_s$, where H_i is the average heterozygosity across loci in the invasive population and H_s is the same value calculated for the putative source region) is only about 17% across a broad range of animal introductions, with most values

TABLE 9.1 *Loss of genetic diversity in naturalized animal populations*

Species	F	A	Reference
<i>Passer montanus</i>	0.174	-0.05	St. Louis and Barlow 1988
<i>Carduelis chloris</i>	0	-0.025	Merilä et al. 1996
<i>Fringilla coelebs</i>	-0.375	-0.035	Baker 1992
<i>Passer domesticus</i>	0.057	0.167	Parkin and Cole 1985
<i>Acridotheres tristis</i>	0.193	0.210	Baker and Moeed 1987
<i>Sturnus vulgaris</i> *	0	0.283	Ross 1983; Cabe 1998
<i>Carpodacus mexicanus</i> *	0.036	—	Wang et al. 2003
<i>Junco hyemalis</i>	0.125	0.373	Rasner et al. 2004
<i>Thymallus thymallus</i>	0.561	0.581	Koskinen et al. 2002
<i>Linepithema humile</i>	0.681	0.492	Tsutsui et al. 2000
<i>Drosophila subobscura</i> *	0.098	0.623	Balanyà et al. 1994; Pascual et al. 2001
<i>Musca autumnalis</i>	0.2	0.063	Bryant et al. 1981
<i>Solenopsis richteri</i>	0.33	0.25	Ross and Trager 1990
<i>Solenopsis invicta</i>	0.226	0.183	Ross et al. 1993
<i>Ceratitis capitata</i> *	0.656	0.648	Malacrida et al. 1998
<i>Ceratitis rosa</i>	0.051	0.241	Baliraine et al. 2004
<i>Dreissena polymorpha</i> *	-0.117	-0.077	Boileau and Hebert 1992; Stepien et al. 2002
<i>Carcinus maenas</i> *	0.189	0.478	Bagley and Geller 1999
<i>Perna perna</i>	0.109	0.053	Holland 2001
<i>Theba pisana</i>	0.5	0.2	Johnson 1988
<i>Littorina saxatilis</i>	0.125	0	Janson 1987
<i>Bosmina coregoni</i>	-0.111	0	Demelo and Hebert 1994
<i>Bythotrephes longimanus</i>	-0.042	0	Berg et al. 2002
<i>Marenzelleria viridis</i> *	0.029	0.058	Rohner et al. 1996
<i>Crepidula fornicata</i>	0.114	-0.098	Dupont et al. 2003
<i>Peromyscus leucopus</i>	0.125	0	Browne 1977
<i>Macropus rufogriseus</i>	0.097	0.244	Le Page et al. 2000
<i>Anolis grahami</i>	0.250	0.167	Taylor and Gorman 1975
<i>Rana ridibunda</i>	-0.067	0.187	Zeisset and Beebee 2003

Note: This table includes species for which allelic data from both source and invasive populations, along with the proportional loss of heterozygosity (F) and allelic diversity (A) from each species invasion, are available. The asterisk (*) indicates averaged effects across introductions to multiple locations or multiple studies of the same introduction. If not recognized, multiple introductions to the same region will tend to reduce the proportional loss of diversity, potentially shifting some values lower relative to the actual effects of the bottleneck. Those introduced populations that have higher diversity than putative source populations, shown here as negative values, may represent admixture of multiple propagules. Because sampling artifacts may also generate biased values of F , the “average” F (0.17) given in the text considers these negative values to be equivalent to 0; however, the average including these cases in which diversity is higher in the non-native range is similar (0.15). Some of these studies demonstrate that extremely low diversity may occur in both populations and that small changes in heterozygosity may result in large proportional changes (e.g., *Theba pisana*, $H_{\text{source}} = 0.10$, $H_{\text{introduced}} = 0.05$), which may bias F upward for such examples.

Figure 9.2 Proportional loss of (A) heterozygosity and (B) allelic diversity in invasive populations relative to their source populations. The proportional loss of heterozygosity, averaging about 0.17 across the studies listed in Table 9.1, is frequently used as a measure of the strength of a bottleneck (F). However, several of these studies suggest that the loss of rare alleles is more evolutionarily significant and a more sensitive indicator of what happens to invasive populations as they recover from a bottleneck; in most of the studies summarized in B, the loss of allelic diversity is also modest (< 20% loss). Note that for both A and B, several studies listed in the leftmost column (i.e., 0, < 0.2) have negative values (i.e., show a proportional gain in heterozygosity or number of alleles); these values may reflect the effects of genetic admixture or may be due to sampling artifacts (see Table 9.1 for details).



being considerably lower. Comparisons based on allelic diversity suggest that founder effects may have a slightly greater effect on the loss of rare alleles (Figure 9.2B).

Why, in terms of genetic diversity assayed through neutral markers, do introduced populations appear to differ so little from their sources? A variety of theoretical studies of colonization suggest that the effects of a bottleneck on genetic diversity can be relatively small. Consider the following example: genealogical simulations suggest that if a small founding population of 20–100 individuals rapidly expands following establishment, allelic diversity, heterozygosity, and mean time to common ancestry among individuals drop only slightly below their values in the source population (Austerlitz et al. 1997). On the other hand, if new populations are initiated by sequential colonizations of a few individuals from one population to the next, then genetic diversity can appreciably decline (also see Nei et al. 1975; Barton 1989). Studies of a natural colonization time series in an island-colonizing bird, the Australian silvereye (*Zosterops lateralis*), confirm these predictions (Clegg et al. 2002). Comparison of each recently established population with its immediate

source revealed no significant differences in terms of either allelic diversity or heterozygosity; only comparisons between the earliest colonists and the most recent expansion populations showed significant differentiation. Thus, both in theory and in practice, the influence of genetic drift and founder effects on genetic diversity may have been overemphasized for many colonization events.

Given the minimal effects of species introduction on genetic diversity in introduced populations, there are only a few convincing empirical examples of drift influencing the evolution of traits that might facilitate the spread or differentiation of introduced species (Lee 2002). If levels of variation at neutral markers are strongly correlated with the additive genetic variance harbored by a population, this would suggest that the population dynamics of introduction and invasion typically do not translate into significant genetic change (Amos and Balmford 2001; Dupont et al. 2003). However, the stronger effects of bottlenecks and drift on allelic diversity (as opposed to heterozygosity per se) may be especially important when rare alleles influence fitness (Leberg 1992; Ross et al. 1993; Tsutsui et al. 2000; Box 9.2).

BOX 9.2 *Small Changes, Big Effects: The Importance of Genetic Details (and Why Additive Genetic Variance May Tell Only Part of the Story)*

The invasion of the red fire ant (*Solenopsis invicta*) incisively illustrates how small genetic changes can have profound evolutionary consequences (Lee 2002; Tsutsui and Suarez 2003). The red fire ant was originally introduced into the United States in the 1930s; however, it was not until the 1970s that the more ecologically destructive multi-queen (polygyne) colonies appeared and the species spread widely (Krieger and Ross 2002). The genetics underlying gyne number in *S. invicta* help explain this time lag between the initial introduction and spread: single-queen (monogyne) colonies are homozygous (*BB*) at the “Gp-9” locus, whereas polygyne colonies are heterozygous (*Bb*). Monogyne colonies produce new *BB* queens that disperse to found new monogyne colonies, and polygyne colonies generate *BB*, *Bb*, and *bb* queens (although *Bb* are generally the most successful).

Apparently, a secondary introduction brought the *b* allele into U.S. populations, leading to colony dynamics that fueled the spread of red fire ants (Krieger and Ross 2002).

The dramatic social and ecological changes following the addition of a single allele to a resident introduced population of *S. invicta* underscore why metrics that reflect genetic changes averaged across the entire genome (e.g., additive genetic variance), especially those based on presumably neutral markers (e.g., heterozygosity, allelic diversity), may not accurately predict how evolution may proceed during an invasion. For example, Ross et al. (1993) compared changes in diversity at putatively neutral allozyme markers (Baer 1999) with diversity at sex-determining loci in source and invasive populations of fire ants. Although the bottleneck associated with the invasion appears to have had a minimal effect on levels

So, do introduced populations possess sufficient additive genetic variance to respond rapidly to selection? The tentative answer at this point is yes. As we previously discussed, the level of additive genetic variance in the introduced population should decline in proportion to the population's inbreeding coefficient, F , which measures the strength of a bottleneck. Unless a bottleneck reduces an introduced population to just a few individuals, and the introduced population remains small for a protracted interval before (or if) it expands, there will be little loss of additive genetic variance (or genetic diversity).

Effects of Introductions and Invasions on Phenotypic Evolution, Fitness, and Population Differentiation

Although it appears that introduction bottlenecks do not typically lead to a major loss of neutral genetic variation (see Figure 9.2), it would be premature to generalize the effects of introduction on neutral markers to its effects on

BOX 9.2 (continued)

of heterozygosity at most genetic loci, estimates of the number of alleles at sex-determining loci suggest that allelic diversity may have dropped by 60%–80% because most alleles in this system are likely to be rare (Ross et al. 1993). Thus, the loss of rare alleles may be a more sensitive indicator of the strength and potential effect of a bottleneck on an invasive population (Leberg 1992; Ross et al. 1993). In addition, the loss of rare alleles may have disproportionately strong effects on the fitness of invasive species, particularly when those alleles are experiencing frequency-dependent selection and affect the expression of mating preferences, social organization, sex determination, or life history traits (Ross et al. 1993; Hiscock 2000; López-Fanjul et al. 2003).

Despite the potential, in theory, for bottlenecks and drift to influence levels of genetic variation in newly founded populations, to our knowledge there is only one well-documented example suggesting that the loss of genetic variation has affected a trait that im-

proves the fitness of members of an invasive species. Tsutsui et al. (2001) document a significant reduction in allelic variation at microsatellite loci in populations of the Argentine ant (*Linepithema humile*) in its introduced, compared with its native, range. To the extent that this reduction in genetic diversity at presumably neutral microsatellite loci in *Linepithema* corresponds to a loss in variation at loci that influence the precision of kin and nestmate recognition, a genetic bottleneck appears to have promoted a shift in colony social structure from small, mutually aggressive colonies in the species' native range to large, nonaggressive multi-queen supercolonies in the introduced range that attain high population densities (Tsutsui and Suárez 2003). Because the formation of supercolonies reduces intraspecific competition, this bottleneck appears to have facilitated the ability of introduced Argentine ants to successfully outcompete native ant species (Holway 1999).

genetic variation for fitness-related traits (McKay and Latta 2002; López-Fanjul et al. 2003). While our literature search (see Figure 9.2 and Table 9.1) suggests that the overall genetic background of an introduced population does not differ substantially from that of its source population(s), the loss of even a few alleles could, in principle, significantly constrain or facilitate evolution. However, simply placing a relatively unchanged genetic background in a different environment with different species interactions could also generate novel phenotypic responses (Coyne 1994). When a single population is the source for an introduced population, the expressed phenotypic variance of the newly founded population will often change in predictable ways related to the strength of the bottleneck and the nature of the selective regime. However, if previously isolated populations from the source range interbreed in the introduced range, interactions between distinct genetic backgrounds may generate novel phenotypes. In this section, we evaluate how small genetic changes, selection on traits tied to fitness, and novel genetic environments influence the phenotypic evolution and fitness of introduced populations.

Effects of population bottlenecks

The argument is far from settled over whether a population's failure or success following introduction depends primarily on demographic effects, such as stochastic variation in population size that increases extinction probability when census size is small and variable, or on genetic effects, such as increased inbreeding depression or the loss of additive genetic variance, which may limit the ability of a species or population to respond to further changes in the biotic and physical environment. Some insights regarding the relative importance of demographic and genetic effects might be gained by comparing the effects of population bottlenecks following a species introduction with those of bottlenecks associated with endangered species. There is, however, one key difference: introduced species that become successful invaders often pass through short-lived bottlenecks followed by rapid population expansion, whereas endangered species often remain at low effective population sizes for extended periods (Allendorf and Lundquist 2003).

A recent study by Briskie and Mackintosh (2004) clearly showed that inbreeding depression due to bottlenecks significantly affects the fitness of both endangered and invasive bird species in New Zealand. Specifically, bird populations that had passed through bottlenecks of fewer than 150 individuals experienced significantly lower egg hatching success than source populations that had not experienced a bottleneck in population size (Briskie and Mackintosh 2004). Similar negative effects of bottlenecks on competitive ability and other components of fitness occur in invasive plants and other organisms with histories of small effective population size (Saccheri et al. 1998; Knaepkens et al. 2002; Bossdorf et al. 2004). Thus, although levels of heterozygosity and allelic diversity may not change dramatically with moderate bottlenecks (Briskie and Mackintosh 2004; see also Nei et al. 1975; Amos and

Balmford 2001), the expression of deleterious recessive alleles appears to be greater in these inbred populations.

The expression of particular alleles may be modified strongly by their interaction with alleles at other genetic loci. Although the process of “conversion” of epistatic variance to additive genetic variance does not generate novel alleles, it can allow more direct expression of existing allelic variation. While overall, little allelic diversity may be lost due to a bottleneck (see Figure 9.2B), rare alleles may change in frequency or be lost (Brookes et al. 1997), and the phenotypic effect of one allele or gene could effectively increase or decrease due to reduced variation at one or more epistatically associated loci (Brodie 2000). In many ways, the fitness effects of these rare or frequency-dependent alleles are at the heart of the debate over the relative importance of drift and selection for evolutionary diversification (Coyne et al. 1997; Goodnight and Wade 2000). Some studies focus on founder events that may have eliminated alleles maintained by frequency-dependent or sexual selection (see Box 9.2). Consequently, there are circumstances under which drift *can* have a major effect on the evolutionary responses of an introduced or invasive population, even without greatly influencing overall levels of additive genetic variance.

Effects of hybridization and introgression

Most novel epistatic interactions that arise from admixture or hybridization should reduce fitness (Barton 1989; Willett and Burton 2003). However, the occasional expression of “hybrid vigor” suggests that positive interactions—which could improve the mean fitness of an invasive population—may arise when previously isolated lineages hybridize and introgress. In some cases, it appears that hybridization can lead to the formation of new species through a variety of either ecological or genetic mechanisms that reduce or eliminate backcrossing, and therefore gene flow, with parental stocks (reviewed in Dowling and Secor 1993; Ellstrand and Schierenbeck 2000; Gaskin and Schaal 2002; Rieseberg et al. 2003). Alternatively, the hybrids may backcross with native species to such an extent that they essentially “absorb” the parental stocks through introgression (Ellstrand and Schierenbeck 2000). Introgression of non-native genes into native species (as well as established agricultural stocks), especially when it involves genetically modified organisms, is of more than academic interest (Stewart et al. 2003; Roderick and Navajas 2003) because the process may alter economically and ecologically desirable characteristics of native and domesticated species. In its extreme form, introgressive hybridization may lead to the genetic extinction of native species (Rosenfield and Kodric-Brown 2003).

Introgressive hybridization can also provide important insights into the evolution of reproductive isolation. One of the most challenging issues in the study of speciation is whether allopatric (geographically disjunct) taxa are, in fact, reproductively incompatible (the criterion for species status under the biological species concept; see Coyne and Orr 2004). For all but a handful of taxa,

it is generally impossible (and unethical) to bring allopatric taxa into sympatry and examine the mechanisms that limit or promote genetic exchange between those taxa in more or less natural (compared with laboratory) surroundings. Yet this is what introductions represent, so they can be useful for analyzing the role of mating behavior and recognition cues in reproductive isolation. For instance, sexual selection for aggressive mating behavior appears to have driven the extensive introgression between native and introduced pupfishes (*Cyprinodon*) in New Mexico and Texas (Rosenfield and Kodric-Brown 2003). Female Pecos pupfish (*C. pecosensis*) prefer the aggressive mating behavior of non-native males to that of their own species, a preference that probably reflects an ancestral bias rather than a contemporary adaptation. Hybrid offspring share the aggressive mating behavior of the invasive parent species, and so continue to drive the introgression of these species. Thus, patterns of introgression, while representing a significant conservation threat, can also inform our understanding of reproductive isolation and speciation (see Rice and Sax, this volume).

Extensive introgression following hybridization is not a foregone conclusion. Successful introgression of non-native genes often requires strong selection favoring hybrid phenotypes or behaviors, or linkage to advantageous alleles that generates overdominance (Stewart et al. 2003; Rosenfield and Kodric-Brown 2003; Bernatchez and Landry 2003). Nevertheless, both direct and indirect evidence, primarily from crop plants, demonstrates that genetic markers move from crop species to native plants and vice versa (Ellstrand et al. 1999; Stewart et al. 2003). Studies of introgression also suggest that the complex interactions between genetic background and environmental variation on phenotypic variation and fitness, and their subsequent effects, often produce a hybrid genome that is a heterogeneous blend of the parental genomes (Harrison 1990; Rieseberg et al. 2003).

Additive genetic variance and phenotypic responses to selection

Many factors, some environmental, some genetic, contribute to an organism's phenotype. Consequently, it is important when measuring changes in the phenotypic composition of newly founded populations to separate the contributions of environmental, additive, and nonadditive genetic effects (López-Fanjul et al. 2003). For example, although phenotypic divergence outpaces divergence of molecular markers during the process of invasion by grayling (Koskinen et al. 2002), it remains unclear what proportion of phenotypic divergence results from selection on additive genetic variance, environmental contributions to phenotypic differentiation, or nonadditive interactions.

Grayling, of course, are not the only organisms that exhibit major phenotypic changes during introductions and invasions (reviewed in Ellstrand and Schierenbeck 2000; Lee 2002; Müller-Schärer et al. 2004). Although some of the observed changes appear to result from eco-phenotypic responses to novel environments (e.g., Sexton et al. 2002), selection in natural populations may be

quite effective at generating rapid and heritable phenotypic evolution (Reznick and Ghalambor 2001). Indeed, a recent review of field selection experiments demonstrated a mean selection gradient of about 16% (Kingsolver et al. 2001). It seems likely that selection gradients acting on introduced populations could be just as steep, if not steeper (Whitlock 1997). In terms of response to these selection gradients, overwhelming evidence demonstrates that many populations can, and do, evolve in novel selective regimes at surprisingly rapid rates (Kingsolver et al. 2001; Reznick and Ghalambor 2001). While the evidence from introduced and invasive species is potentially biased because it necessarily focuses on *successful* introductions and invasions, it nevertheless suggests that rapid evolution of introduced species is possible, even for populations that have passed through significant bottlenecks. Again, the question is whether population bottlenecks sufficiently reduce additive genetic variance to the point that mechanisms other than selection in a novel environment should be invoked.

Several recent studies directly confront this question, and their results indicate that introduced populations possess sufficient additive genetic variance (despite losses due to genetic bottlenecks) to respond rapidly to selection. For example, within two decades of the introduction of *Drosophila subobscura* into the Americas, the wing length of introduced North American females had significantly increased with latitude, mirroring a previously documented pattern in native European *D. subobscura* (Huey et al. 2000; Huey et al., this volume). However, in North American populations, this phenotypic cline resulted from changes in the relative lengths of different parts of the wing than in Europe, suggesting that sufficient additive genetic variance was present in both source and invasive populations to permit genetically independent, but phenotypically equivalent, responses to a comparable environmental gradient. This necessary level of genetic variation appears to have been maintained with an introduced propagule of only about a dozen individuals (Pascual et al. 2001).

Other studies (e.g., Grant et al. 2001; Rasner et al. 2004) also suggest that the magnitude and duration of bottlenecks that accompany successful introductions are often not severe enough to prevent substantial phenotypic evolution of invading species entering novel environments and communities. Even in the most extreme cases studied—in which a single pair of individuals has founded a new population—the resulting population can respond to selection. Following colonization of the Galápagos island of Daphne Major by the large ground finch (*Geospiza magnirostris*) in 1982—an event in which only a single breeding pair successfully colonized—the population grew in size rapidly, being supplemented by only low levels of immigration (Grant et al. 2001). With these dynamics, there was no net decline in heterozygosity at 16 microsatellite loci, yet there was a dramatic heritable shift in beak shape after only 9 years. Grant et al. (2001) argue that both drift and selection were involved in the phenotypic and fitness responses of the successful colonists, as the success and/or fitness of colonists was in part determined by levels of heterozygosity in the newly founded population, as well as by the identity of the source population.

Post-introduction immigration in this and other similar circumstances may have supplemented the additive genetic variance in the founder population, and at the same time reduced the effects of inbreeding depression by limiting the expression of recessive deleterious alleles. In addition, ongoing immigration may buffer introduced populations from extinction due to demographic stochasticity.

From Population Differentiation to Speciation

What can introductions and invasions tell us about the contributions of founder effects, drift, and selection to the evolution of reproductive isolation and speciation? The available data suggest that most introduced species—examples of small populations that have become established—are capable of responding to selection and genetically diverging from their source populations. Some biologists (e.g., Mayr 1963; Carson 1968; Templeton 1980) have extended Wright's shifting balance theory and emphasis on the importance of drift in evolution by suggesting that speciation itself is promoted by strong founder events that generate novel templates for selection to act on. Following the loss of allelic diversity associated with a bottleneck, genes that had evolved in the context of a polymorphic genetic background would subsequently interact in a new, more homozygous genetic environment. These changes could then lead to selection favoring novel epistatic interactions (a "genetic revolution" *sensu* Mayr 1954) that lead to rapid evolutionary change. This outcome is largely driven by intrinsic genetic interactions; however, any introduced or recently founded population is also likely to experience a different environment and selective regime, which would confound attempts to separate the effects of genetic interactions from the effects of the environment (Coyne 1994).

In addition to the difficulty of separating the effects of genetic interactions and of novel environmental factors, there are several other reasons to question the generality of speciation theories in which drift provides the primary force driving divergence between populations (Coyne 1994). For example, Barton (1989) showed that when the inbreeding coefficient F is less than 0.2 (as with most of the examples from introduced populations in Figure 9.2), more divergence between populations can be explained by selection acting on post-bottleneck additive genetic variance than can be explained by either drift or higher-order (dominance and epistatic) genetic interactions. It is noteworthy that an important distinction between arguments favoring the primacy of Fisherian mass selection and those promoting the importance of drift-related evolutionary phenomena is whether the additive effects of alleles are more or less constant regardless of the allelic composition of the population (Goodnight and Wade 2000). Barton and Turelli (2004) argue that even if the conversion of epistatic and dominance interactions is detectably strong, the stochastic variance of this conversion process makes it less important than the overall amount of purely additive variance that passes through a bottleneck.

Overall, loss of genetic variation due to founder effects and genetic drift seems to play a minor role in the success of most species introductions, as well as natural colonization sequences (Clegg et al. 2002; Cox 2004). When multiple source populations contribute to an invasion, a relative increase in allelic diversity or novel allelic combinations in these genetic admixtures appears to increase the likelihood that new lineages will arise and succeed in an introduced range (Grant et al. 2001; Novak and Mack, this volume). Garcia et al. (1989) showed that, with respect to allele frequencies at a number of loci, invasive Californian populations of the slender wild oat *Avena barbata* are not distinct from ancestral source populations in Spain. However, the data suggest that selection in the introduced range has involved a “reorganization of the ancestral allelic ingredients of the Spanish gene pool into novel multilocus allelic combinations adapted to specific habitats” (Garcia et al. 1989). The shifting balance theory could in part explain the rise of novel multilocus allelic combinations; however, the observed changes are also easily attributable to mass selection acting on the increased additive genetic variance found in post-introduction admixtures of populations derived from distinct source regions.

The available data cannot resolve the ongoing debate on the importance of Fisherian mass selection versus Wright’s shifting balance theory (and related models that emphasize the role of drift). It has been argued (Goodnight and Wade 2000; Skipper 2002) that neither model is intended to be a general description of evolution, and the relative importance of one or the other may vary from one biological example to the next. What does seem clear is that introduced species often exhibit dramatic phenotypic changes that are comparatively larger than the changes observed in the same populations at neutral loci. Thus, selection is likely to be an important force in most examples of evolutionary change in small populations (Orr and Orr 1996; Huey et al. 2000; Koskinen et al. 2002; Lee 2002; McKay and Latta 2002; Rasner et al. 2004).

Conclusions and Prospects

The extent to which natural and anthropogenically generated bottlenecks facilitate or inhibit evolutionary change has generated an enduring debate in both evolutionary and conservation biology. Evolutionary geneticists, including Mayr (1954) and Templeton (1980), championed the idea that founder effects occurring in peripheral or isolated populations could promote “genetic revolutions,” resulting in striking phenotypic change and perhaps even speciation. However, Barton (1989) argued that the trade-off between the apparent reduction of genetic variation from a source to a founder population and the amount of phenotypic variance that selection in the founder population could act on limits the generality of this effect (also see Coyne 1994; Rice and Hostert 1993). The resolution of this controversy remains elusive; however, theoretical analyses of invasion scenarios and empirical comparisons of genetic variation in introduced populations with that in source population(s) offer powerful

insights into the effects of founder events and isolation on evolutionary change, precisely because these introductions represent extreme examples of evolution in small isolated populations. Our synthesis shows that in general, the effect of founder events on neutral, and perhaps fitness-related, variation is not extreme: introduced populations often retain 80% or more of the genetic variation present in their source(s).

Perhaps this information will help to resolve a paradox: invasive species often displace resident species that should be better adapted to their native environments (Allendorf and Lundquist 2003). Most species are restricted to well-defined geographic distributions, even when it appears that natural dispersal mechanisms could transport them beyond their current distributions. This observation suggests that there *are* limits to a species' ability to respond to the selective forces imposed by novel environments (Fisher 1930; Antonovics 1976; Kirkpatrick and Barton 1997). Levels of genetic variation in introduced populations may be high enough, particularly if multiple source populations are involved, to respond quickly to local patterns of selection on short time scales (Huey et al. 2000; Kingsolver et al. 2001; Lee 2002; Rasner et al. 2004). The evolutionary potential of native species, on the other hand, may be constrained by local adaptation to the longer-term fluctuations in environmental conditions that historically characterize their environment (Schemske and Bierzychudek 2001; Allendorf and Lundquist 2003).

As we see it, one of the major gaps that remains to be filled lies between our growing understanding of how the demography of introductions and invasions affects neutral genetic variation, and how these same demographic processes affect the genes that control the expression of phenotypic traits that are the targets of selection. In an era of increasing availability of genomic data, it should become possible to use closely related model organisms to begin to identify those genes responsible for phenotypic changes during introductions and invasions and to determine more directly whether such changes represent the outcomes of selection. When enough homologous markers (both neutral and with known fitness consequences) can be screened, our ability to distinguish founder effects from strong selection in novel habitats will improve dramatically. At the current rates of species introduction (Sakai et al. 2001) and environmental change (Walther et al. 2002), we are likely to have plenty of opportunities to test our most fundamental models of evolution in the near future.

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Literature Cited

- Allendorf, F. W., and L. L. Lundquist. 2003. Introduction: Population biology, evolution, and control of invasive species. *Conservation Biology* 17:24–30.
- Amos, W., and A. Balmford. 2001. When does conservation genetics matter? *Heredity* 87:257–265.
- Anderson, E. C., and E. A. Thompson. 2002. A model-based method for identifying species hybrids using multilocus genetic data. *Genetics* 160:1217–1229.
- Anttila, C. K., R. A. King, C. Ferris, D. R. Ayres, and D. R. Strong. 2000. Reciprocal hybrid formation of *Spartina* in San Francisco Bay. *Molecular Ecology* 9:765–770.
- Antonovics, J. 1976. The nature of limits to natural selection. *Annals of the Missouri Botanical Gardens* 63:224–247.
- Arnold, M. L. 1997. *Natural hybridization and evolution*. Oxford Series in Ecology and Evolution, Oxford University Press, Oxford.
- Austerlitz, F., B. Jung-Muller, B. Godelle, and P.-H. Gouyon. 1997. Evolution of coalescence times, genetic diversity and structure during colonization. *Theoretical Population Biology* 51:148–164.
- Avise, J. C. 2000. *Phylogeography*. Harvard University Press, Cambridge, MA.
- Ayres, D. R., D. Garcia-Rossi, H. G. Davis, and D. R. Strong. 1999. Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). *Molecular Ecology* 8:1179–1186.
- Baer, C. F. 1999. Among-Locus Variation in Fst: Fish, Allozymes, and the Lewontin-Krakauer Test Revisited. *Genetics* 152:653–659.
- Bagley, M. J., and Geller, J. B. 1999. Microsatellite DNA analysis of native and invading populations of European green crabs. In J. Pederson, ed. *Marine bioinvasions. Proceedings of the First National Conference.*, pp. 241–244. M.I.T. Sea Grant College Program, Cambridge, MA.
- Baker, A. J. 1992. Genetic and morphometric divergence in ancestral European and descendant New Zealand populations of chaffinches (*Fringilla coelebs*). *Evolution* 46:1784–1800.
- Baker, A. J., and A. Moeed. 1987. Rapid genetic differentiation and founder effect in colonizing populations of common Mynas (*Acridotheres tristis*). *Evolution* 41:525–538.
- Balanyà, J., C. Segarra, A. Prevosti, and L. Serra. 1994. Colonization of America by *Drosophila subobscura*: the founder event and a rapid expansion. *Journal of Heredity* 85:427–432.
- Baliraine, F. N., M. Bonizzoni, C. R. Guglielmino, E. O. Osir, S. A. Lux, F. J. Mulaa, L. M. Gomulski, L. Zheng, S. Quilici, G. Gasperi, and A. R. Malacrida. 2004. Population genetics of the potentially invasive African fruit fly species, *Ceratitis rosa* and *Ceratitis fasciventris* (Diptera: Tephritidae). *Molecular Ecology* 13:683–695.
- Bartlett, E., S. J. Novak, and R. N. Mack. 2002. Genetic variation in *Bromus tectorum* (Poaceae): Differentiation in the eastern United States. *American Journal of Botany* 89:602–612.
- Barton, N. H. 1989. Founder effect speciation. In D. Otte, and J. A. Endler, eds., *Speciation and its consequences*, pp. 229–256. Sinauer Associates, Sunderland, MA.
- Barton, N. H., and M. Turelli. 2004. Effects of allele frequency changes on variance components under a general model of epistasis. *Evolution* 58:2111–2132.
- Bastrop, R., K. Jurss, and C. Sturmabauer. 1998. Cryptic species in a marine polychaete and their independent introduction from North America to Europe. *Molecular Biology and Evolution* 15:97–103.
- Berli, P., and J. Felsenstein. 1999. Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Genetics* 152:763–773.
- Bertorelle, G., and L. Excoffier. 1998. Inferring admixture proportions from molecular data. *Molecular Biology and Evolution* 15:1298–1311.
- Bohonak, A. J., N. Davies, F. X. Villablanca, and G. K. Roderick. 2001. Invasion genetics of New World medflies: testing alternative colonization scenarios. *Biological Invasions* 3:103–111.
- Boileau, M. G., and Hebert, P.D. N. 1992. Genetics of the zebra mussel, *Dreissena polymorpha*, in populations from the Great Lakes region and Europe. In T. F. Nalepa, and D. W. Schloesser, eds. *Zebra mussels: Biology, impact, and control*, pp. 227–238. Lewis Publishers, Chelsea, MI.
- Bossdorf, O., D. Prati, H. Auge, and B. Schmid. 2004. Reduced competitive ability in an invasive plant. *Ecology Letters* 7:346–353.
- Briskie, J. V., and M. Mackintosh. 2004. Hatching failure increases with severity of population bottle-

- necks in birds. *Proceedings of the National Academy of Sciences USA* 101:558–561.
- Brodie III, E. D. 2000. Why evolutionary genetics does not always add up. In J. B. Wolf, E. D. Brodie III, and M. J. Wade, eds., *Epistasis and the evolutionary process*, pp. 3–19. Oxford University Press, Oxford.
- Brookes, M. I., Y. A. Graneau, P. King, O. C. Rose, C. D. Thomas, and J. L. B. Mallet. 1997. Genetic analysis of founder bottlenecks in the rare British butterfly *Plebejus argus*. *Conservation Biology* 11:648–661.
- Browne, R. A. 1977. Genetic variation in island and mainland populations of *Peromyscus leucopus*. *American Midland Naturalist* 97:1–9.
- Bryant, E. H., Vandijk, H. and W. Vandelden. 1981. Genetic variability of the face fly, *Musca autumnalis* DeGeer, in relation to a population bottleneck. *Evolution* 35:872–881.
- Cabe, P. R. 1998. The effects of founding bottlenecks on genetic variation in the European starling (*Sturnus vulgaris*) in North America. *Heredity* 80:519–525.
- Carlton, J. T. 1982. The historical biogeography of *Littorina littorea* on the Atlantic coast of North America and implications for the interpretation of the structure of New England intertidal communities. *Malacological Review* 15:146.
- Carson, H. L. 1968. The population flush and its genetic consequences. In R. C. Lewontin, ed. *Population biology and evolution*, pp. 123–138. Syracuse University Press, Syracuse, NY.
- Cheverud, J. M. 2000. Detecting epistasis among quantitative trait loci. In J. B. Wolf, E. D. Brodie III, and M. J. Wade, eds. *Epistasis and the evolutionary process*, pp. 58–81. Oxford University Press, Oxford.
- Chikhi, L., M. W. Bruford, and M. A. Beaumont. 2001. Estimation of admixture proportions: a likelihood-based approach using Markov chain Monte Carlo. *Genetics* 158:1347–1362.
- Choisy, M., P. Franck, and J.-M. Cornuet. 2004. Estimating admixture proportions with microsatellites: comparison of methods based on simulated data. *Molecular Ecology* 13:955–968.
- Clegg, S. M., S. M. Degnan, J. Kikkawa, C. Moritz, A. Estoup, and I. P. F. Owens. 2002. Genetic consequences of sequential founder events by an island-colonizing bird. *Proceedings of the National Academy of Sciences USA* 99:8127–8132.
- Cox, G. W. 2004. *Alien species and evolution: The evolutionary ecology of exotic plants, animals, microbes, and interacting native species*. Island Press, Washington, DC.
- Coyne, J. A. 1994. Ernst Mayr and the origin of species. *Evolution* 48:19–30.
- Coyne, J. A., N. H. Barton, and M. Turelli. 1997. Perspective: a critique of Sewall Wright's shifting balance theory of evolution. *Evolution* 51:643–71.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Sunderland, MA.
- Davies, N., F. X. Villablanca, and G. K. Roderick. 1999. Determining the source of individuals: multilocus genotyping in nonequilibrium population genetics. *Trends in Ecology and Evolution* 14:17–21.
- Demelo, R., and P. D. N. Hebert. 1994. Founder effects and geographical variation in the invading cladoceran *Bosmina (Eubosmina) coregoni* Baird 1857 in North America. *Heredity* 73:490–99.
- Dowling, T. E., and C. L. Secor. 1997. The role of hybridization in the evolutionary diversification of animals. *Annual Review of Ecology and Systematics* 28:593–619.
- Dupont, L., D. Jollivet, and F. Viard. 2003. High genetic diversity and ephemeral drift effects in a successful introduced mollusc (*Crepidula fornicata*: Gastropoda). *Marine Ecology-Progress Series* 253:183–95.
- Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants. *Proceedings of the National Academy of Sciences USA* 97:7043–7050.
- Ellstrand, N. C., H. C. Prentice, and J. F. Hancock. 1999. Gene flow and introgression from domesticated plants into their wild relatives. *Annual Review of Ecology and Systematics* 30:539–563.
- Estoup, A., I. J. Wilson, C. Sullivan, J. M. Cornuet, and C. Moritz. 2001. Inferring population history from microsatellite and enzyme data in serially introduced cane toads, *Bufo marinus*. *Genetics* 159:1671–1687.
- Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. *Theoretical Population Biology* 3:87–112.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford.
- Garcia, P., F. J. Vences, M. Pérez De La Vega, and R. W. Allard. 1989. Allelic and genotypic composition of ancestral Spanish and colonial Californian gene pools of *Avena barbata*: Evolutionary implications. *Genetics* 122:687–694.
- Gaskin, J. F., and B. A. Schaal. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proceedings of the National Academy of Sciences USA* 99:11256–11259.
- Goodnight, C. J. 1988. Epistasis and the effect of founder events on the additive genetic variance. *Evolution* 42:441–54.
- Goodnight, C. J. 2000. Modeling gene interaction in structured populations. In J. B. Wolf, E. D. Brodie, and M. J. Wade, eds. *Epistasis and the evolutionary process*, pp. 58–81. Oxford University Press, Oxford.
- Goodnight, C. J. and M. J. Wade. 2000. The ongoing synthesis: a reply to Coyne, Barton, and Turelli. *Evolution* 54:317–324.
- Grant, P. R., B. R. Grant, and K. Petren. 2001. A population founded by a single pair of individuals: estab-

- ishment, expansion, and evolution. *Genetica* 112/113:359–382.
- Grosberg, R. K., and C. W. Cunningham. 2001. Genetic structure in the sea: from populations to communities. In M. D. Bertness, M. E. Hay, and S. D. Gaines, eds. *Marine community ecology*, pp. 61–84 Sinauer Associates, Sunderland, MA.
- Guinand, B., A. Topchy, K. S. Page, M. K. Burnham-Curtis, W. F. Punch, and K. T. Scribner. 2002. Comparisons of likelihood and machine learning methods of individual classification. *Journal of Heredity* 93:260–269.
- Hansen, M. M., E. E. Nielsen, D. Bekkevold, and K.-L. D. Mensberg. 2001. Admixture analysis and stocking impact assessment in brown trout (*Salmo trutta*), estimated with incomplete baseline data. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1853–1860.
- Harrison, R. G. 1990. Hybrid zones: Windows on evolutionary process. In D. J. Futuyma and J. Antonovics, eds. *Oxford Surveys in Evolutionary Biology* 7:69–128.
- Hebert, P. D. N., and M. E. A. Cristescu. 2002. Genetic perspectives on invasions: the case of the *Cladocera*. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1229–1234.
- Hiscock, S. J. 2000. Genetic control of self incompatibility in *Senecio squalidus* L. (Asteraceae)—a successful colonising species. *Heredity* 84:10–19.
- Holland, B. S. 2001. Invasion Without a Bottleneck: Microsatellite Variation in Natural and Invasive Populations of the Brown Mussel *Perna perna* (L). *Marine Biotechnology* 3:407–415.
- Holway, D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80:238–251.
- Hudson, R. R. 1990. Gene genealogies and the coalescent process. In D. J. Futuyma, and J. Antonovics, eds. *Oxford Surveys in Evolutionary Biology* pp. 1–44.
- Huey, R., G. W. Gilchrist, and M. Carlsen. 2000. Rapid evolution of a latitudinal cline in body size in an introduced fly. *Science* 287:308–309.
- Janson, K. 1987. Allozyme and shell variation in two marine snails (*Littorina, Prosobranchia*) with different dispersal abilities. *Biological Journal of the Linnaean Society* 30:245–257.
- Johnson, M. S. 1988. Founder effects and geographic variation in the land snail *Theba pisana*. *Heredity* 61:133–142.
- Johnson, M. T. J., and A. A. Agrawal. 2003. The ecological play of predator-prey dynamics in an evolutionary theatre. *Trends in Ecology and Evolution* 18:549–556.
- Keightley, P. D., and M. Lynch. 2003. Toward a realistic model of mutations affecting fitness. *Evolution* 57:683–685.
- Kingman, J. F. C. 1982. On the genealogy of large populations. *Journal of Applied Probability* 19a:27–43.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *American Naturalist* 157:245–261.
- Kirkpatrick, M. and N. H. Barton. 1997. Evolution of a species' range. *American Naturalist* 150:1–23.
- Knaepkens, G., D. Knapen, L. Bervoets, B. Hänfling, E. Verheyen, and M. Eens. 2002. Genetic diversity and condition factor: a significant relationship in Flemish but not in German populations of the European bullhead (*Cottus gobio* L.). *Heredity* 89:280–287.
- Knowles, L. L. 2004. The burgeoning field of statistical phylogeography. *Journal of Evolutionary Biology* 17:1–10.
- Kolbe, J. J., R. E. Glor, L. R. Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431:177–181.
- Koskinen, M. T., T. O. Haugen, and C. R. Primmer. 2002. Contemporary Fisherian life-history evolution in small salmonid populations. *Nature* 419:826–830.
- Krieger, M. J. B., and K. G. Ross. 2002. Identification of a major gene regulating complex social behavior. *Science* 295:328–332.
- Le Page, S. L., R. A. Livermore, D. W. Cooper, and A. C. Taylor. 2000. Genetic analysis of a documented population bottleneck: introduced Bennett's wallabies (*Macropus rufogriseus rufogriseus*) in New Zealand. *Molecular Ecology* 9:753–763.
- Leberg, P. L. 1992. Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. *Evolution* 46:477–494.
- Lee, C. E. 1999. Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. *Evolution* 53:1423–1434.
- Lee, C. E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* 17:386–391.
- López-Fanjul, C., A. Fernández, and M. A. Toro. 2003. The effect of neutral nonadditive gene action on the quantitative index of population divergence. *Genetics* 164:1627–1633.
- Luikart, G., P. R. England, D. Tallmon, S. Jordan, and P. Taberlet. 2003. The power and promise of population genomics: from genotyping to genome typing. *Nature Reviews in Genetics* 4:981–994.
- Malacrida, A. R., F. Marinoni, C. Torti, L. M. Gomulski, F. Sebastiani, C. Bonvicini, G. Gasperi, and C. R. Guglielmino. 1998. Genetic aspects of the worldwide colonization process of *Ceratitidis capitata*. *Journal of Heredity* 89:501–507.

- Maruyama, T., and P. A. Fuerst. 1984. Population bottlenecks and nonequilibrium models in population genetics. I. Allele numbers when populations evolve from zero variability. *Genetics* 108:745–763.
- Mayr, E. 1954. Change of genetic environment and evolution. In J. S. Huxley, A. C. Hardy, and E. B. Ford, eds. *Evolution as a process*, pp. 156–180. Allen and Unwin, London.
- Mayr, E. 1963. *Animal species and evolution*. Harvard University Press, Cambridge, MA.
- McKay, J. K., and R. G. Latta. 2002. Adaptive population divergence: markers, QTL and traits. *Trends in Ecology and Evolution* 17:285–291.
- Merilä, J., M. Björklund, and A. J. Baker. 1996. The successful founder: genetics of introduced *Carduelis chloris* (greenfinch) populations in New Zealand. *Heredity* 77:410–422.
- Müller-Schärer, H., U. Schaffner, and T. Steinger. 2004. Evolution in invasive plants and implications for biological control. *Trends in Ecology and Evolution* 19:417–422.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1–10.
- Nei, M. 1987. *Molecular evolutionary genetics*. Columbia University Press, New York.
- Orr, H. A., and L. H. Orr. 1996. Waiting for speciation: the effect of population subdivision on the time to speciation. *Evolution* 50:1742–1749.
- Otto, S. P., and M. C. Whitlock. 1997. Fixation of beneficial mutations in a population of changing size. *Genetics* 146:723–733.
- Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- Parkin, D. T., and S. R. Cole. 1985. Genetic differentiation and rates of evolution in some introduced populations of the House Sparrow, *Passer domesticus* in Australia and New Zealand. *Heredity* 54:15–23.
- Pascual, M., C. F. Aquadro, V. Soto, and L. Serra. 2001. Microsatellite variation in colonizing and palearctic populations of *Drosophila subobscura*. *Molecular Biology and Evolution*. 18:731–740.
- Rasner, C. A., P. Yeh, L. S. Eggert, K. E. Hunt, D. S. Woodruff, and T. D. Price. 2004. Genetic and morphological evolution following a founder event in the dark-eyed junco, *Junco hyemalis thurberi*. *Molecular Ecology* 13:671–681.
- Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about conditions that promote adaptive evolution. *Genetica* 112:183–198.
- Rice, W. R. and E. E. Hostert. 1993. Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* 47:1637–1653.
- Rieseberg, L. H., O. Raymond, D. M. Rosenthal, Z. Lai, K. Livingstone, T. Nakazato, J. L. Durphy, A. E. Schwarzbach, L. A. Donovan, and C. Lexer. 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. *Science* 301:1211–1216.
- Roderick, G. K., and M. Navajas. 2003. Genes in new environments: Genetics and evolution in biological control. *Nature Reviews in Genetics* 4:889–899.
- Rohner, M., R. Bastrop, and K. Jurs. 1996. Colonization of Europe by two American genetic types or species of the genus *Marenzelleria* (Polychaeta: Spionidae). An electrophoretic analysis of allozymes. *Marine Biology* 127:277–287.
- Rosenfield, J. A., and A. Kodric-Brown. 2003. Sexual selection promotes hybridization between Pecos pupfish, *Cyprinodon pecosensis* and sheepshead minnow, *C. variegatus*. *Journal of Evolutionary Biology*. 16:595–606.
- Ross, H. A. 1983. Genetic differentiation of starling (*Sturnus vulgaris*: Aves) populations in New Zealand and Great Britain. *Journal of the Zoological Society of London* 201:351–362.
- Ross, K. G., E. L. Vargo, L. Keller, and J. C. Trager. 1993. Effect of a founder event on variation in the genetic sex-determining system of the fire ant *Solenopsis invicta*. *Genetics* 135:843–854.
- Ross, K. G. and J. C. Trager. 1990. Systematics and population genetics of fire ants (*Solenopsis saevissima* complex) from Argentina. *Evolution* 44:2113–2134.
- Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* 392:491–494.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. Mccauley, P. O’Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305–332.
- Schemske, D. W., and P. Bierzychudek. 2001. Perspective: Evolution of flower color in the desert annual *Linanthus parryae*: Wright revisited. *Evolution* 55:1269–1282.
- Sexton, J. P., J. K. McKay, and A. Sala. 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecological Applications* 12:1652–1660.
- Skipper, R. A. 2002. The persistence of the R. A. Fisher–Sewall Wright controversy. *Biology and Philosophy* 17:341–367.
- St. Louis, V. L., and J. C. Barlow. 1988. Genetic differentiation among ancestral and introduced populations of the Eurasian tree sparrow (*Passer montanus*). *Evolution* 42:266–276.
- Stepien, C. A., C. D. Taylor, and K. A. Dabrowska. 2002. Genetic variability and phylogeographical patterns of a nonindigenous species invasion: A

- comparison of exotic vs. native zebra and quagga mussel populations. *Journal of Evolutionary Biology* 15:314–328.
- Stewart, C. N., M. D. Halfhill, and S. I. Warwick. 2003. Transgene introgression from genetically modified crops to their wild relatives. *Nature Reviews in Genetics* 4:806–817.
- Stockwell, C. A., and M. V. Ashley. 2004. Rapid adaptation and conservation. *Conservation Biology* 18:272–273.
- Taylor, C. E., and G. C. Gorman. 1975. Population genetics of a “colonizing” lizard: natural selection for allozyme morphs in *Anolis grahami*. *Heredity* 35:241–247.
- Templeton, A. R. 1980. The theory of speciation via the founder principle. *Genetics* 94:1011–1038.
- Tsutsui, N. D., A. V. Suarez, D. A. Holway, and T. J. Case. 2000. Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences USA* 97:5948–5953.
- Tsutsui, N. D., A. V. Suarez, D. A. Holway, and T. J. Case. 2001. Relationships among native and introduced populations of the Argentine ant (*Linepithema humile*) and the source of introduced populations. *Molecular Ecology* 10:2151–2161.
- Tsutsui, N. D., and A. V. Suarez. 2003. The colony structure and population biology of invasive ants. *Conservation Biology* 17:48–58.
- Turner, T. F., J. P. Wares, and J. R. Gold. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics* 162:1329–1339.
- Wade, M. J., and C. J. Goodnight. 1998. Perspective: The theories of Fisher and Wright in the context of metapopulations: when nature does many small experiments. *Evolution* 52:1537–1553.
- Wakeley, J., and J. Hey. 1997. Estimating ancestral population parameters. *Genetics* 145:847–855.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Waples, R. S. 1989. A generalized approach for estimating effective population size from temporal changes in allele frequency. *Genetics* 121:379–391.
- Wang, Z., A. J. Baker, G. E. Hill, and S. V. Edwards. 2003. Reconciling actual and inferred population histories in the house finch (*Carpodacus mexicanus*). *Evolution* 57:2852–2864.
- Wares, J. P., D. S. Goldwater, B. Y. Kong, and C. W. Cunningham. 2002. Refuting a controversial case of a human-mediated marine species introduction. *Ecology Letters* 5:577–584.
- Whitlock, M. C. 1995. Two-locus drift with sex chromosomes: the partitioning and conversion of variance in subdivided populations. *Theoretical Population Biology* 48:44–64.
- Whitlock, M. C. 1997. Founder effects and peak shifts without genetic drift: adaptive peak shifts occur easily when environments fluctuate slightly. *Evolution* 51:1044–1048.
- Whitlock, M. C., and K. Fowler. 1999. The changes in genetic and environmental variance with inbreeding in *Drosophila melanogaster*. *Genetics* 152:345–353.
- Willett, C. S., and R. S. Burton. 2003. Environmental influences on epistatic interactions: viabilities of cytochrome *c* genotypes in interpopulation crosses. *Evolution* 57:2286–2292.
- Willis, J. H., and H. A. Orr. 1993. Increased heritable variation following population bottlenecks: The role of dominance. *Evolution* 47:949–957.
- Wolf, J. B., E. D. Brodie III, and M. J. Wade, eds. 2000. *Epistasis and the evolutionary process*. Oxford University Press, Oxford.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the 6th International Congress on Genetics* 1:356–366.
- Zeisset, I., and T. J. C. Beebee. 2003. Population genetics of a successful invader: the marsh frog *Rana ridibunda* in Britain. *Molecular Ecology* 12:639–646.