

CHAPTER 16

Evolutionary rescue under environmental change?

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Overview

When environmental conditions change, the persistence of populations will depend on phenotypic responses that better suit individuals for the new conditions. Such responses can occur through individual-level behavioural or plastic changes, or population-level evolutionary changes (including population-level changes in behaviour and plasticity). Many studies have now documented adaptive phenotypic responses to environmental change, but very few have investigated their potential role in making the difference between population persistence versus extirpation (i.e. evolutionary rescue). We explore these topics by focusing on key questions about evolutionary rescue and the limitations of this process. In doing so, we outline pressing research questions and potential empirical approaches to their resolution.

16.1 Introduction

For populations to persist, they need to be at least reasonably well adapted for the local environmental conditions. That is, the set of phenotypic traits present in the population must yield high enough mean population fitness to maintain a stable population size. This is presumably the situation in most natural populations found in relatively constant environments. When environmental conditions change, however, existing phenotypes are expected to be less well adapted, potentially causing population declines to the point of local extirpation or even range-wide extinction. This mismatch between current phenotypes and those that would yield high fitness in the new environment imposes a pressure on individuals and populations to reduce the mismatch, which can then increase fitness and population size. In short, phenotypic changes can make the difference between persistence and extirpation in the face of environmental change.

Phenotypes can become better matched to altered environmental conditions in several different ways.

Most immediately, individuals can alter their behaviour to reduce exposure to the new conditions—or otherwise ameliorate its potentially detrimental effects. Many instances of such immediate behavioural responses are discussed in this book, and so we here mention only a few exemplars: individuals can (1) move to more appropriate locations (e.g. Bowler and Benton 2005) (see Chapter 5), (2) alter their behaviour to reduce susceptibility to new predators (e.g. Poethke et al. 2010) (see Chapters 7, 10, and 14), or select a more appropriate nesting site (e.g. Eggers et al. 2006; Rushbrook et al. 2010) (see Chapter 8). But such immediate behavioural responses will not always be sufficient to prevent population declines. For instance, behaviours that evolved under previous conditions may be maladaptive under new conditions (e.g. evolutionary ‘traps’: Schlaepfer et al. 2002; Visser 2008). Or behaviours might simply be ineffective, such as when appropriate locations are no longer available. Our goal in the present chapter is to ask what happens in these situations where immediate behavioural responses will not do the trick.

When immediate behavioural responses are insufficient, two other options are possible for reducing the mismatch between existing phenotypes and those favoured under new conditions. First, phenotypes can be altered developmentally, such as through phenotypic plasticity, maternal effects, or various other non-genetic phenotypic alterations (Bonduriansky and Day 2009; Piglucci 2001, see also Chapter 11). Although these developmental changes (henceforth just ‘plasticity’) can be a particularly rapid way to recover fitness following environmental change (Parmesan 2006), they are not all powerful. The reason is that plasticity is sometimes maladaptive (Grether 2005) or, when adaptive, can be subject to costs (DeWitt et al. 1998) and limits (Visser 2008). Thus, although plasticity will be an important response to environmental change, it will not always be sufficient to maintain or recover high fitness.

The ultimate solution to environmental change is for populations to evolve such that their phenotypes are better suited for the new conditions (Fig. 16.1). In contrast to the individual-level phenotypic changes achievable through behaviour or plasticity, evolutionary changes in phenotypes require cross-generational shifts in allele frequency. It is obvious that evolutionary changes have been a critical part of the evolution of biological diversity through Earth’s history, but the extent to which they will be helpful in the face of future environmental change remains uncertain. Historically, evolution was considered too slow to be relevant on short time scales, such as years or decades. Recently, however, a number of examples have come to light of adaptive evolution occurring on precisely these time frames (reviewed in Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Hendry et al. 2008). Uncertainty remains, however, as to just how common such changes are and how important they are for population persistence: that is, so-called ‘evolutionary rescue’ (Gomulkiewicz and Holt 1995; Bell and Gonzalez 2009, 2011).

In the present chapter, we investigate how evolutionary (genetic) change can alter phenotypes (adaptively or maladaptively) in ways that can then influence population persistence. We do so by examining several key questions and then a set of

potential constraints on this process. We do not focus on immediate behavioural responses or on individual phenotypic plasticity, because these are covered elsewhere in the book (e.g. Chapter 11). We do, however, consider the *evolution* of behaviour and plasticity in response to environmental change. The difficulty in determining the genetic basis and evolution of behaviour (Skinner 1966; Clutton-Brock and Harvey 1985) means that such examples are relatively rare. Thus, although we must usually refer to non-behaviour examples, the basic principles should apply to any sort of trait, including behaviour.

16.2 Key questions

To discuss issues surrounding evolutionary responses to environmental change, we focus on five key questions: how important is genetic (as opposed to plastic) change, to what extent will plasticity evolve, is evolution fast enough to prevent substantial maladaptation, does evolution stem from standing genetic variation or new mutations, and how many genes are likely to be involved?

16.2.1 How important is genetic (as opposed to plastic) change?

The answer to this question will depend on properties of the environment (e.g. the rate and magnitude of change and availability of alternative habitats), the organism (e.g. natural history, population size, and dispersal ability), and the relevant traits (e.g. genetic variance and the potential for plasticity) (Holt 1990). No simple generalizations are possible given that empirical evidence for the importance of genetic change versus plasticity is limited and opinions are divided (Bradshaw and McNeilly 1991; Gienapp et al. 2008; Visser 2008). Part of the uncertainty stems from a scarcity of research simultaneously quantifying both phenotypic and genetic responses to a given environmental change. Instead, the vast majority of studies simply quantify phenotypic changes, the genetic basis for which remains uncertain (reviewed in Darimont et al. 2009; Hendry et al. 2008; Hendry and Kinnison 1999; Root et al. 2003; Westley 2011). To illustrate issues surrounding

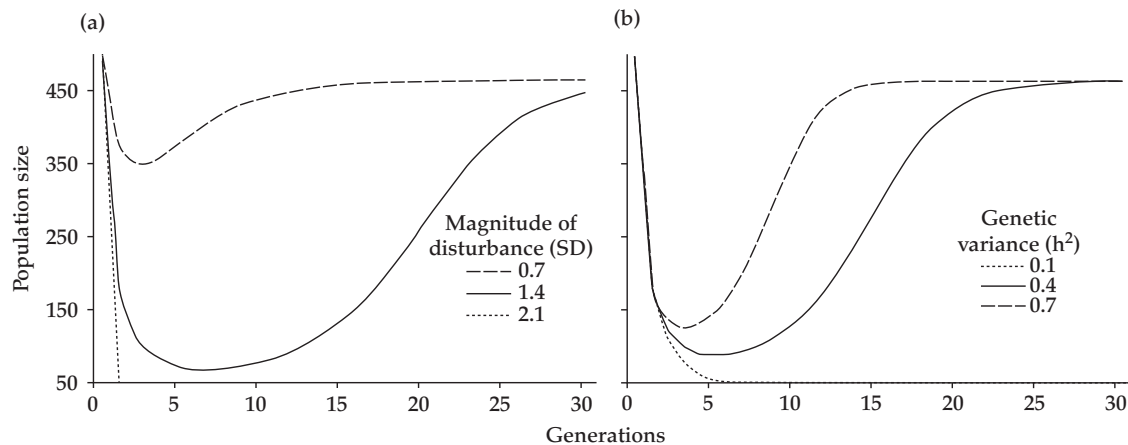


Figure 16.1 Illustrations of evolutionary rescue derived from a deterministic quantitative-genetic model. A well-adapted population experiences an environmental perturbation that causes a decline in average fitness and a reduction in population size. As in Gomulkiewicz and Holt (1995), extinction is assumed to occur stochastically when the population size drops to below a certain size, here 50 individuals. Without evolution (not shown), the maladapted population declines quickly toward extirpation. With evolution, the population can adapt and eventually recover population size. The potential for this evolutionary rescue depends on a number of factors. Those illustrated here are the magnitude of the environmental disturbance (a) and the amount of genetic variance in the population (b). The magnitude of disturbance is indexed as the difference between the current and optimal population mean value in units of phenotypic standard deviation (SD). The genetic variance is measured as heritability ($h^2 = V_A/V_P$). In (a), $h^2 = 0.3$. In (b) the magnitude of environmental change is 0.6 SD. These results are obtained by perturbing the optimum trait value in the model of Hendry (2004).

this endeavour, we here concentrate on studies of responses to climate warming.

One reason why so few studies have disentangled the genetic versus plastic responses to climate change is that the standard inferential approaches are difficult to implement in a temporal context. For instance, common-garden experiments are typically used to confirm a genetic foundation for phenotypic differences, but such experiments are difficult for groups sampled in different years, because they cannot then be raised or grown together. One potential solution is to provide identical common-garden conditions in the different years, such that the different groups experience the same conditions despite not being contemporaneous. This approach is rarely applied but, in one example, Bradshaw and Holzapfel (2001) reared pitcher plant mosquitoes *Wyeomyia smithii* from the same populations under identical laboratory conditions in 1972 and 1996. They found that the photoperiodic response (developmental timing in relation to photoperiod) had evolved in the direction expected to be adaptive under climate warming. A related strategy is to use

dormant seeds (Franks et al. 2007) or resting eggs (Cousyn et al. 2001) to resurrect individuals from the past for direct comparison to individuals in the present. More such studies are needed.

An alternative to common-garden studies is to use long-term data from pedigreed natural populations in statistical models that can separate maternal, plastic, and genetic contributions to phenotypic change. Specifically, by comparing patterns seen across years within individuals to those seen across generations, it becomes possible to disentangle the contributions of plasticity and evolution (Kruuk 2004; Nussey et al. 2005). In an early example of this approach, Przybylo et al. (2000) analysed individual breeding performance in collared flycatchers *Ficedula albicollis* and demonstrated that population level responses to climate warming could be entirely attributed to phenotypic plasticity. Similar work in other species has confirmed that birds do often possess the ability to respond plastically to changing environmental conditions (Charmantier et al. 2008; Nussey et al. 2005; Reed et al. 2006; see also Chapter 11). At the same time, these methods do sometimes

document evolutionary change. For example, Réale and colleagues (2003) showed that changes in parturition dates in Canadian red squirrels *Tamiasciurus hudsonicus* experiencing warmer spring temperatures were 87% plastic and 13% evolutionary (genetic). Some evolution has clearly occurred in this and other situations but the relative amount remains an open question in the majority of studies (Hadfield et al. 2010).

Although phenotypic plasticity can accomplish a substantial amount of phenotypic change, it will not always be enough. For example, Phillimore et al. (2010) showed that the plastic responses of common frog *Rana temporaria* breeding times to temperature are much lower than those required to maintain locally-adaptive phenotypes under expected climate warming. Evolution will thus be necessary. In addition to such arguments that ‘plasticity will not be enough’, several studies have confirmed changes in allele frequencies in response to climate change. These include temporal shifts in chromosomal arrangements and candidate gene allele frequencies for *Drosophila* populations experiencing climate warming (Balanya et al. 2006; Umina et al. 2005). Similarly, studies of the tree species *Fagus sylvatica* have shown predictable allele frequency changes with temperature (Jump et al. 2006). But the inferences possible in such studies remain limited—because they typically lack information relating specific genetic changes to phenotypes relevant for fitness under changing conditions. Overall, however, these and the above studies demonstrate that a number of natural populations have evolved in response to altered climate.

In summary, many studies have documented phenotypic responses to climate change, but few have been able to separate genetic from plastic effects. Indeed, our presentation focused on climate change to highlight a situation where this ambiguity is particularly acute. By contrast, studies documenting phenotypic responses to other types of environmental change have generally had an easier time confirming genetic effects (reviewed by Hendry and Kinnison 1999; Kinnison and Hendry 2001; Hendry et al. 2008). And a number of these other contexts involve examples of the evolution of behaviour, such as antipredator behaviour in

Trinidadian guppies *Poecilia reticulata* (Magurran et al. 1992) and *Daphnia* (Cousyn et al. 2001), migratory behaviour in birds (Berthold et al. 1992) and toads (Phillips et al. 2010), and host plant choice in insects (Singer et al. 1993). Overall, then, evolution is an important part of responses to environmental change, including in some climate change situations (Bradshaw and Holzapfel 2006; Gienapp et al. 2008; Skelly et al. 2007). However, much more work needs to be done on interactions between evolution and plasticity, particularly because various authors have suggested that plasticity (and behaviour) can either dampen or enhance selection, and thereby modify evolutionary trajectories (e.g. Huey et al. 2003; Ghalambor et al. 2007).

16.2.2 Will plasticity evolve?

In the previous section, we set plasticity and evolution against each other as alternative ways in which phenotypes might change in response to altered environments. We also noted that both processes can jointly contribute to phenotypic change. Here we wish to make the additional point that plasticity can itself evolve—and this process could make a key contribution to evolutionary rescue.

Lande (2009) modelled an abrupt shift in the optimum phenotype for a population showing plasticity in that phenotype. As expected, mean fitness of the population at first declined dramatically because the original phenotypes were poorly suited to the new environment. Fitness then increased to some extent owing to the adaptive plastic responses of individuals—but not greatly so because the plastic response was limited. Over the generations that followed, the most dramatic evolutionary response was in the trait’s plasticity: individuals with the highest plasticity were favoured because they were the ones that could produce phenotypes closest to the new optimum. This evolution of plasticity led to a rapid recovery of fitness. Then, once most individuals could plastically achieve the new phenotype, plasticity decreased through time (because plasticity was not very efficient) to be replaced with genetic changes in the non-plastic component of the trait (a process called genetic assimilation). This model, and others that followed (Chevin and Lande

2010; Chevin et al. 2010), thus predict that the evolution of plasticity should be particularly important for populations facing environmental change.

Empirical studies have certainly shown that plasticity often evolves in natural populations facing environmental change (Crispo et al. 2010; Van Doorslaer et al. 2009)—but this is not universal. Recent long-term studies of two pedigreed populations of great tits *Parus major* provide an opportunity to illustrate the alternatives. In a Dutch population (Nussey et al. 2005), (1) individuals differed dramatically in their plasticity for reproductive date, (2) selection driven by climate warming favoured increased plasticity, and (3) current levels of plasticity were insufficient for attaining optimal reproductive timing. In this case, we would expect the evolution of plasticity to be an important part of future responses to warming conditions. In a UK population (Charmantier et al. 2008), (1) individuals did not differ strongly in plasticity, (2) plasticity was not under selection, and (3) the existing plastic response was sufficient for attaining optimal reproductive timing. In this case, we would not expect the evolution of plasticity, perhaps because selection is acting to maintain plasticity at a close to optimal value. In short, the importance of the evolution of plasticity in responding to environmental change could vary widely—even among populations of a single species.

16.2.3 Is evolution fast enough?

Adaptive evolution might prevent population declines and extirpation if it increases mean absolute fitness enough to counter the fitness decline caused by environmental change (Burger and Lynch 1995; Gomulkiewicz and Holt 1995; Bell and Gonzalez 2009, 2011). A first point to consider in this process of evolutionary rescue is the extent to which environmental change initially decreases mean absolute fitness. In particular, a greater shift in the optimum and stronger stabilizing selection around that optimum both increase ‘selection load’ (i.e. the reduction in mean fitness incurred as a result of selection), which can then decrease population size. It is difficult to directly assess this process in nature. Indirectly, however, most extirpations must ulti-

mately be the consequence of maladaptation of one form or another—and environmental changes have certainly caused many extirpations (Hughes et al. 1997). As an illustrative example, in freshwater lakes that became acidified owing to industrial pollution, only a minority of species in the original community were able to persist by evolving higher tolerance to the lower pH (Bradshaw and McNeilly 1991). And several other studies have related declines in population size to increasing maladaptation of key traits (Both et al. 2006; Portner and Knust 2007).

A second point to consider in the process of evolutionary rescue is the potential for adaptive evolutionary responses, which will generally depend on the availability of relevant additive genetic variance (Fisher 1930). Standing genetic variance is expected to increase with increasing population size and gene flow, and to decrease with increasing directional or stabilizing selection (Bell 1997; Futuyma 2010; Hartl and Clark 1997). Although standing genetic variation in fitness related traits is common in natural populations, it still might be insufficient to accomplish the necessary evolution—as will be discussed later. In such cases, the probability of adaptation will depend on the supply rate of new beneficial mutations, and population size will again be a crucial parameter (Gomulkiewicz and Holt 1995; Lynch and Lande 1993; Orr and Unckless 2008). Regardless of its source (pre-existing standing variation or *de novo* mutations—more about this below), higher levels of relevant genetic variance will typically allow population persistence in the face of greater environmental change—by making it possible for the population to more closely and quickly match the phenotypic optimum (Fig. 16.1; Gomulkiewicz and Holt 1995; Holt and Gomulkiewicz 2004).

Environmental change can be either abrupt or sustained. In the abrupt case, adaptive evolution needs to arrest the population decline quickly enough to forestall extirpation. If evolutionary rescue occurs, phenotypes in the population are expected to eventually match the new optimum—as long as that optimum remains stable (Gomulkiewicz and Holt 1995; Lande 2009; Fig. 16.1). In the sustained case, adaptive evolution needs to prevent the

mean phenotype from lagging so far behind the changing optimum that severe negative population growth occurs. If evolutionary rescue occurs, the expectation is a steady state in which the mean phenotype lags a reasonably consistent distance behind the continually changing optimum. A model by Bürger and Lynch (1995) predicted that the 'critical rate' of environmental change (change in the phenotypic optimum) required to prevent extirpation is on the order of 10% of a phenotypic standard deviation per generation, although under some conditions this rate drops closer to 1%.

The specification of a 'critical rate', makes it tempting to compare with observed rates of phenotypic change in natural populations. For example, strong natural selection on Darwin's finches *Geospiza fortis* during a drought resulted in evolutionary responses of 0.66 'haldanes' (phenotypic standard deviations per generation) for beak depth and 0.71 haldanes for body size (Grant and Grant 2006). These rates clearly exceed the suggested critical rate of 0.10 and, indeed, 85% of the population died in a single year. By contrast, rates of phenotypic change in most other studies are typically less than 0.10 haldanes (Hendry and Kinnison 1999; Hendry et al. 2008) and are often not accompanied by population declines (Reznick and Ghalambor 2001). Perhaps in these cases, phenotypic change has been sufficiently fast to counter the demographic costs of initial maladaptation. Despite this illustrative argument, we caution against straight-up comparisons of theory-derived critical rates to observed rates of change in natural populations. The reason is that the specification of a critical rate requires many unrealistic assumptions, such as perpetual persistence under constant environmental change. Critical rates for natural populations over time frames of conservation interest could be very different.

Adaptation to a new environment will almost always involve many phenotypic traits. Given the impossibility of measuring all such traits, most studies tend to focus on one or a few traits thought to be of critical importance. As one example, Pulido and Berthold (2010) monitored migratory behaviour in a population of blackcaps *Sylvia atricapilla* to test for evolutionary responses to recent climate

change. Using a common garden experiment, they demonstrated a genetic change towards residency (as opposed to migration) and the evolution of phenotypic plasticity in migration timing. They then used an artificial selection experiment to show that residency evolves in initially migratory populations under selection for a shorter migration. As a second example, Barrett and colleagues (2011) estimated the rate of evolution of temperature tolerance in three-spined sticklebacks *Gasterosteus aculeatus*. They first documented heritable differences in cold tolerance between natural marine and freshwater populations: the latter could tolerate the colder conditions typical of that environment. They then showed that marine fish introduced into freshwater ponds converged on the cold tolerance typical of freshwater populations in only three generations (Fig. 16.2). The observed rate of change of 0.63 haldanes was among the fastest rates recorded in natural populations (by comparison to the data in Hendry and Kinnison 1999). Even so, all of the experimental stickleback populations went extinct during a particularly cold winter, and so evolution, even if very rapid, might not save populations facing altered environmental conditions.

The study of key traits is certainly valuable, but it is also useful to consider overall adaptation by examining changes in major fitness components. The reason is that evolutionary rescue will depend most directly on fitness itself, to which many phenotypic traits will generally contribute. So a more direct route to inferring the potential for evolutionary rescue might be to measure how evolution improves mean population fitness. This is very difficult to accomplish for natural populations—but some studies at least have been able to measure how evolution alters major fitness components of individuals. For instance, Gordon et al. (2009) showed that evolution in introduced guppy populations improved survival rates by up to 50% over 13–26 generations, although plasticity might also have made a contribution. Even more dramatically and directly, Kinnison et al. (2008) showed that the evolution of introduced Chinook salmon *Oncorhynchus tshawytscha* populations improved reproductive output in local environments by up to 150% over 26 generations. In both cases, changes in

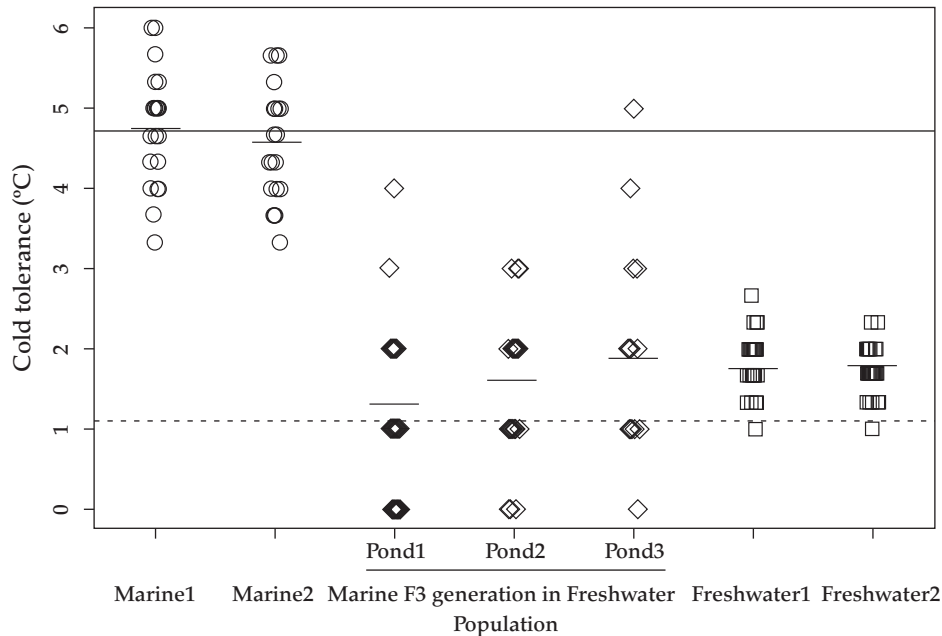


Figure 16.2 Experimental evolution of cold tolerance in three-spined stickleback. Circles and squares indicate individual fish from natural marine and freshwater populations, respectively. Diamonds indicate individual fish from three experimental freshwater ponds that were colonized with wild marine fish three generations previously and have evolved to have similar cold tolerance as natural freshwater populations. (Although evolution is likely, common-garden experiments were not used to confirm it.) Dashed lines show minimum temperatures in nature from 11 marine sites (solid) and 14 freshwater lakes (dashed). Bars indicate population mean values. Modified from Barrett et al. 2011.

major fitness components were markedly greater than changes in individual phenotypic traits thought to be under divergent selection.

In summary, factors likely to influence whether or not adaptive evolution will save populations from extirpation are now reasonably well known from theoretical models. Evidence also now exists from natural populations of noteworthy adaptive changes in specific traits, many of which could contribute to population growth. However, few of these studies involved populations in any apparent danger of extirpation—and so the direct implications for evolutionary rescue are uncertain. We therefore need studies of natural populations that specifically relate the factors thought to be important for evolutionary rescue to whether or not evolutionary rescue actually occurs. This is not a trivial endeavour, of course, because it requires replicated experimental studies, such as have been implemented in the laboratory (e.g. Bell and Gonzalez

2009; Bell and Gonzalez 2011). At present, the closest analogues we have are *ad hoc* ‘experiments’ that consider which species survive when environments change and whether those species showed the evolution of traits thought to be important in the new conditions (Bradshaw and McNeilly 1991).

16.2.4 Standing genetic variation versus new mutations?

As noted in the previous section, evolutionary responses to environmental change could occur through two different genetic routes: selection on pre-existing (‘standing’) genetic variation or on new mutations (Barrett and Schluter 2008). Between these two options, standing variation is likely to allow much faster evolution because it is immediately available when selective conditions change and because the higher initial frequency of pre-existing alleles reduces average fixation time

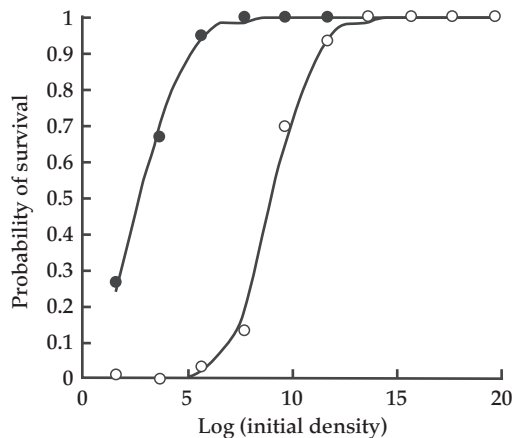


Figure 16.3 Probability of survival over 25 generations of experimental yeast populations abruptly transferred to salt (a stressful environment), in relation to the log of initial population size. Filled circles represent the control (low salt) treatment and open circles represent the high salt treatment. Each point is based on 60 replicate populations. Lines are fitted logistic regressions. Modified from Bell and Gonzalez (2009).

(Hermisson and Pennings 2005; Przeworski et al. 2005). In addition, beneficial alleles present in the standing variation will be older, and so might have accumulated multiple advantageous mutations (McGregor et al. 2007). These alleles might also have been pre-tested by selection in relevant environments (Michel et al. 2007), which increases the chance they will be helpful in the future. All of these arguments suggest that immediate adaptation to environmental change will be predominantly fuelled by standing genetic variation, an assertion supported by some case studies of ecologically relevant genes (Colosimo et al. 2005; Feder et al. 2003; Steiner et al. 2009; Tishkoff et al. 2007).

However, standing genetic variation will not always be sufficient, particularly when populations are very small, inbreeding is high, or genetic variance has been reduced by past selection (Bell and Collins 2008; Lynch and Lande 1993). In these cases, new mutations become crucial and their supply rate will depend heavily on population size—another knock against small populations. Bell and Gonzalez (2009) tested this expectation by conducting experimental evolution studies with yeast to determine how the frequency of mutations capable of rescuing the population under environmental stress (high

concentrations of salt) varied as a function of population size. They first confirmed the expected (Bell and Collins 2008; Bell and Gonzalez 2011; Gomulkiewicz and Holt 1995; Orr and Unckless 2008) U-shaped trajectory of population size: a rapid decline owing to initial maladaptation followed by an increase as new better-adapted genotypes increase in frequency. They then confirmed that evolutionary rescue was more likely to occur in larger populations (Fig. 16.3)—because of the reduced stochastic loss of new beneficial mutations. These results confirm that sufficiently large populations can generate the beneficial mutations necessary for evolutionary rescue under environmental stress. It remains to be seen whether these findings regarding new mutations will hold under more natural conditions in the field.

In summary, adaptation to changing environments will probably often involve standing genetic variation—simply because it is common and immediately available (Hansen and Houle 2008; Roff 2007—but see below). By contrast, new beneficial mutations take more time to arise and then increase in frequency (Hermisson and Pennings 2005; Przeworski et al. 2005), making their contribution most likely when appropriate standing genetic variation is absent, generation times short (e.g. bacteria, viruses, unicellular plants, some arthropods), and the environmental change is not too rapid and abrupt.

16.2.5 How many genes and of what effect?

Based on his geometric model of the adaptive process, Fisher (1930) argued that mutations of small effect have a nearly 50% chance of moving a population toward the local optimum, whereas mutations of large effect have a much lower chance of doing so. This reasoning underlies the common assumption that adaptation consists of fine-tuning the phenotype with very large numbers of genes carrying mutations of relatively small effect (reviewed in Orr 2005). Whether this is typically the case, or whether few genes of large effect are often important, has significant implications for the expected rate of evolutionary response to environmental change.

Reasonable arguments have been advanced both for and against the above two possibilities. On the one hand, theory suggests that advantageous alleles of small effect will take nearly as long as neutral alleles to spread across a subdivided population (Cherry and Wakeley 2003). Waiting for new minor mutations to fix at large numbers of genes might therefore require more time than is available to populations confronted with rapid environmental change (Lynch and Lande 1993). On the other hand, because mutations of small effect are so slow to fix, the genes that carry these mutations are more likely to be polymorphic to start with (Hansen and Houle 2004). Adaptation from standing genetic variation might therefore involve mutations of small effect. In addition, greater numbers of genes contributing to adaptation will reduce the consequences of losing some mutations to stochastic processes. By contrast, evolutionary rescue through a large effect mutation at a single locus requires population sizes large enough and environmental changes gradual enough to prevent stochastic loss of the mutation while it is still rare (Gomulkiewicz and Holt 1995). However, this limitation might be less critical if adaptation can be accomplished by major-effect mutations at any one of multiple interchangeable loci (Orr and Unckless 2008). Similarly, the danger of losing a beneficial allele at a single major effect locus can be reduced if the allele is maintained at relatively high frequency because it is recessive (Orr and Betancourt 2001; Przeworski et al. 2005), mutations producing the allele occur recurrently at the same locus (Pennings and Hermisson 2006a; Pennings and Hermisson 2006b), or selection is balancing (Charlesworth et al. 1997; Hermisson and Pennings 2005).

Overall, theory thus suggests a fairly narrow range of parameter space that permits evolutionary rescue through large effect mutations at single loci. Empirical evidence does suggest, however, that genes of large effect can contribute to adaptation. Examples include genes functionally associated with flowering time in *Arabidopsis thaliana* (FLC; Ehrenreich and Purugganan 2006; Scarcelli et al. 2007), body armour and colouration in three-spined stickleback (*Pitx1*, *Eda*, *Kitlg*; Colosimo et al. 2005), swimming ability and development rate in killifish

(*Fundulus heteroclitus*; *LDH-B*; reviewed by Powers and Schulte 1998), a variety of traits in sulphur butterflies (*Colias eurytheme*; *PGI*; reviewed by Wheat et al. 2006), crypsis in oldfield mice (*Peromyscus polionotus*; *Mc1r*; Hoekstra et al. 2006), albinism in cavefish (*Astyanax mexicanus*; *Oca2*; Protas et al. 2006), and beak dimensions in Darwin's finches (*Geospiza* sp.; *BMP4*; Abzhanov et al. 2004).

With respect to major effect loci affecting behaviour, a good example is the *forager* gene in *Drosophila melanogaster*, which has two alternate alleles that affect movement patterns of larvae between feeding patches (Sokolowski et al. 1997). These alleles are thought to be maintained in natural populations by frequency dependent selection, with the rarer of the two behavioural strategies at advantage in nutrient-poor conditions (Fitzpatrick et al. 2007). Another gene contributing to important behavioural variation is the *v1ar* locus in prairie voles *Microtus ochrogaster*, which has been shown to influence the transition from a polygamous to a more monogamous behaviour through differential expression in the brain (Donaldson and Young 2008). The same gene has been associated with partner fidelity in humans—in a large Swedish population, men homozygous for the *v1ar* variant allele were twice as likely to experience marital discord (Walum et al. 2008). Despite these few compelling examples, studies demonstrating the effects of specific genes on behaviour, whether large or small, have been limited, largely due to the challenges associated with dissecting behaviour genetically.

Studies of single large-effect genes, such as those listed above, have attracted much of the limelight, and in doing so have biased current perceptions about the typical genetics of adaptation. First, in most cases, it isn't clear how many mutations have contributed to the effects of a particular gene. Second, most studies identifying genes through quantitative trait locus (QTL) mapping have only pursued and functionally verified the single gene of largest effect, while ignoring most of the other, perhaps more typical, genes of modest to small effect. Third, candidate gene approaches are, by definition, limited to testing the role of single genes controlling known phenotypes (Haag and True

2001). Even lateral plate number in stickleback, which is often cited as a prime example of a ‘single locus’ trait because of the major effects of *Eda*, is determined by a more complicated inheritance pattern (Cresko et al. 2004). In addition, *Eda*, or a closely linked gene, has effects on other fitness components (Barrett et al. 2008; Marchinko 2009). Moreover, genome scans have made it increasingly clear that many traits that differ adaptively among populations are controlled by numerous genes of very small effect, such as for human height (Yang et al. 2010) and a number of plant traits (Moose et al. 2004; Thumma et al. 2010). Finally, and perhaps most important, all of the existing studies examine the genetics of single traits, whereas overall adaptation to a given environment will often depend on many traits. Thus, even if a single major-effect gene controls a particular adaptive trait, overall adaptation (i.e. fitness) in a given environment will almost certainly be influenced by many genes of small to modest effect.

In summary, the genetics of adaptation to changing environments will vary depending on the circumstances, sometimes involving only a few genes of large effect but other times involving many genes of small effect. At present, we have examples of both situations but their frequency and importance is not yet certain. In the future, increased marker density provided by new genomic tools will greatly facilitate the discovery of minor effect loci and the epistatic interactions between them (Hohenlohe et al. 2010). Also sorely needed are more studies of the genes that determine changes in *fitness*.

16.3 Constraints on evolutionary responses to environmental change

Given that evolution will often be necessary if populations are to maintain high fitness in the face of environmental change, the potential limits to this process will be crucial to understand. These limits must be common given the frequent instances in which populations have been extirpated when environments have changed. We here consider three basic possibilities: limited genetic variation, trait correlations, and ultimate constraints.

16.3.1 Limited genetic variation

Insufficient genetic variation can hamper evolutionary responses to environmental change because the mean phenotype is unable to closely match the optimum, thus increasing the extent to which mean population fitness is compromised (Bürger and Lynch 1995; Orr and Unckless 2008). To make matters worse, the resulting population decline then initiates a detrimental feedback loop: small population sizes increase genetic drift, which reduces genetic variation, which further reduces evolutionary potential (Lynch and Lande 1993).

So just how much relevant genetic variation is present in natural populations? Meta-analyses have repeatedly shown that most traits in most populations do show substantial additive genetic variation and heritability (Hansen and Houle 2008; Roff 2007). However, many of the genetic variants most relevant to adaptation might have been fixed by selection, leaving mostly standing variation that has only small effects on fitness. In addition, levels of variation, and therefore evolvability, depend on environmental conditions and might therefore be higher or lower in particular situations (Hoffmann and Merilä 1999). For all of these reasons, levels of genetic polymorphism (e.g. heritability) of individual traits do not necessarily indicate the potential for evolutionary responses to environmental change. We need more estimates of genetic variance in fitness related traits—and fitness itself—under relevant ecological conditions.

More direct inferences about the sufficiency of genetic variation can be obtained by testing whether or not populations evolve in response to environmental change. One route to such inference is by comparing species that do or do not persist through an environmental change. In one example, only five plant species were able to survive contamination from a copper refinery, and these species showed large evolved changes in copper tolerance (Bradshaw 1984). A number of other plant species that previously coexisted in the same area went extinct, suggesting that a lack of variation for copper tolerance prevented their adaptation to the novel stress. Another route to the above inference is by imposing artificial selection in the direction expected to be favoured under environmental

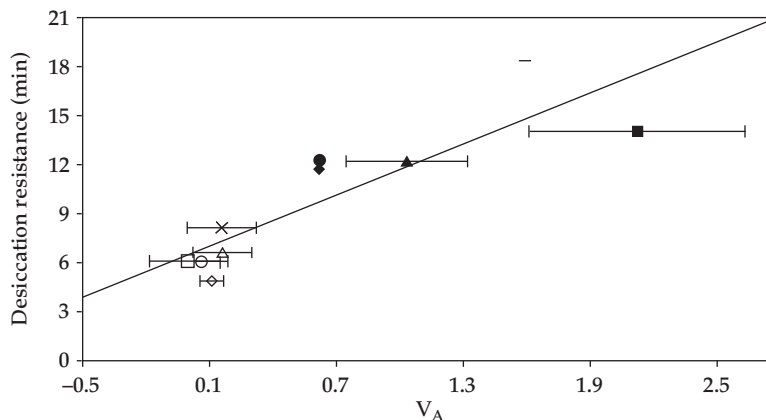


Figure 16.4 Desiccation resistance and additive genetic variance in different *Drosophila* species –, *D. melanogaster*; ●, *D. simulans*; ▲, *D. repleta*; ■, *D. hydei*; ◆, *D. serrata*; ○, *D. birchii*; D. *bunnanda*; □, *D. pseudoananassae*; ×, *D. sulfurigaster*; and ◇, *D. bipunctata*. The key different species have dramatically different genetic variances, with some being essentially zero. Error bars represent 1 SE. Modified from Kellerman et al. (2009). Reprinted with permission from AAAS.

change. In such experiments, adaptive evolution is often observed (Van Doorslaer et al. 2009; Pulido and Berthold 2010) but this is not always so. For example, Hoffman and colleagues (Hoffmann et al. 2003; Kellermann et al. 2009) showed that genetic variance for desiccation resistance, a trait expected to be important under climate change, varies dramatically among *Drosophila* species (Fig. 16.4). At the extreme, the rainforest specialist *Drosophila birchii* failed to evolve increased desiccation resistance even after intense selection for over 30 generations. Existing work thus suggests no general rule can be advanced regarding the likelihood of evolutionary constraints imposed by limited genetic variation. Such constraints will need to be considered on a case-by-case basis.

16.3.2 Trait correlations

Even if relevant genetic variation is ample for individual phenotypic traits, evolution can be constrained by genetic correlations among traits. These correlations could arise through (1) epistatic interactions between genes, (2) genes with pleiotropic effects, or (3) linkage disequilibrium between alleles at loci affecting different traits (Lande 1980; Otto 2004; Weinreich et al. 2005). In the realm of behaviour, genetic correlations likely underlie so-called

‘behavioural syndromes’ (Sih et al. 2004), where a basic behavioural type (e.g. shy versus bold) dictates that individuals cannot simultaneously optimize behaviours for multiple contexts, such as bold during mating but shy in the presence of predators. It is also clear from behavioural screens for mutants that most genes that affect behaviour also have pleiotropic effects on other traits (Pflugelder 1998), often expressed as developmental abnormalities (Sokolowski 2002). These results suggest that the evolution of behaviour could be constrained by deleterious pleiotropic consequences.

When selection is not in the same direction as the correlation between traits (‘antagonistic selection’), the evolutionary response will be constrained (Hansen and Houle 2008; Lande 1979). Such constraints might be relevant in the case of environmental change. Hellmann and Pineda-Krch (2007) simulated the lag between observed phenotypes and optimal phenotypes in a changing environment when fitness was determined by two pleiotropically linked traits. Their analysis confirmed that genetic correlations running counter to the direction of selection increase the lag, and thereby decrease the amount of environmental change a population can tolerate before extirpation. This result echoes the long-standing assumption that greater interdependence of traits (or ‘complexity’) leads to greater levels

of constraint (Fisher 1930). But this assumption might not always hold: for instance, pleiotropy could increase the mutational target size and therefore the evolvability of the trait (Hansen and Houle 2004).

So just how important are these potential constraints for natural populations experiencing environmental change? As one suggestive example, Etterson and Shaw (2001) found that *Chamaecrista fasciculata* legumes subject to drought treatments in a reciprocal transplant experiment were under selection for more and thicker leaves. However, these two traits were negatively genetically correlated, and so most of the variation was orthogonal to the direction of selection. The predicted adaptive evolution was therefore slower than would be expected in the absence of negative genetic correlations. On the flip side, genetic covariances that are high in the same direction as selection could accelerate evolutionary responses—because selection acting on each trait will not only directly influence selection on that trait but also indirectly enhance selection on the other trait (Agrawal and Stinchcombe 2009).

In addition to changing the rate of evolution, genetic correlations could also influence the *direction* of evolution. In particular, evolution could be biased toward the most genetically variable aspects of phenotype (e.g. the ‘genetic lines of least resistance’, Futuyma et al. 1995; Schluter 1996). If so, correlations among traits could cause populations to evolve in directions that are ‘easiest’ but not necessarily the best for improved adaptation. However, empirical studies are strongly divided as to whether or not the direction of evolution is routinely biased by genetic correlations (see citations in Berner et al. 2010). Overall then, it is not yet clear if genetic correlations that limit evolutionary responses to environmental change represent a widespread phenomenon.

16.3.3 Ultimate constraints

Evolutionary constraints can also arise through unbreakable functional or performance trade-offs or strict physiological limits. In the case of trade-offs, adaptation can be limited owing to competing performance requirements, such as speed versus endurance (e.g. Wilson et al. 2002), speed versus force (e.g. Herrel et al. 2009), or stability versus

manoeuvrability (e.g. Weihs 2002). As a particularly ubiquitous trade-off, parents must always compromise between the number of offspring they produce and the size (or quality) of those offspring (Charnov 1995). Similarly, few organisms grow at their physiological maximum (Calow 1982) because they must also allocate resources to other functions, including starvation resistance (Gotthard et al. 1994), metabolic efficiency (Stevens et al. 1998), and skeletal development (Arendt and Wilson 2001).

In the case of strict physiological limits, temperature tolerance has been suggested as a possibility in the case of climate change. For example, although climate warming is expected to be less extreme in the tropics than at higher latitudes, the greater physiological sensitivity of tropical ectotherms means they could experience greater fitness declines (Fig. 16.5; Deutsch et al. 2008). For aquatic organisms, higher temperatures increase oxygen demand but also decrease oxygen supply, until aerobic metabolism becomes insufficient. Pörtner and Knust (2007) have argued that this constraint explains inter-annual variation in the population size of eelpout fish *Zoarces viviparus* in the North and Baltic Seas. Of course, a remaining question is the extent to which current thermal limits cannot be surpassed by evolution. For instance, fishes certainly can adapt to higher temperatures than those currently causing problems for eelpout. At the extreme, Lake Migadi Tilapia *Oreochromis alcalicus grahami* live in 42 °C water, in part because they can breathe air (Franklin et al. 1995). On the other hand, even the dramatic evolution of temperature tolerance in the aforementioned stickleback experiment in subsection 16.2.3 was not enough to prevent extinction under extreme temperatures (Barrett et al. 2011). So temperature tolerance can clearly evolve—but perhaps not always or not quickly enough or far enough.

In summary, shifts in phenotypic optima as a result of environmental change sometimes might not be reachable owing to trade-offs or strict limits imposed by the functional or physiological architecture of whole organisms. Whether or not these limits actually hamper evolutionary rescue in nature is unknown—although upper temperature tolerance is a strong candidate in the case of climate change. In addition, bioenergetic models suggest that geographic distributions may be limited by hard physi-

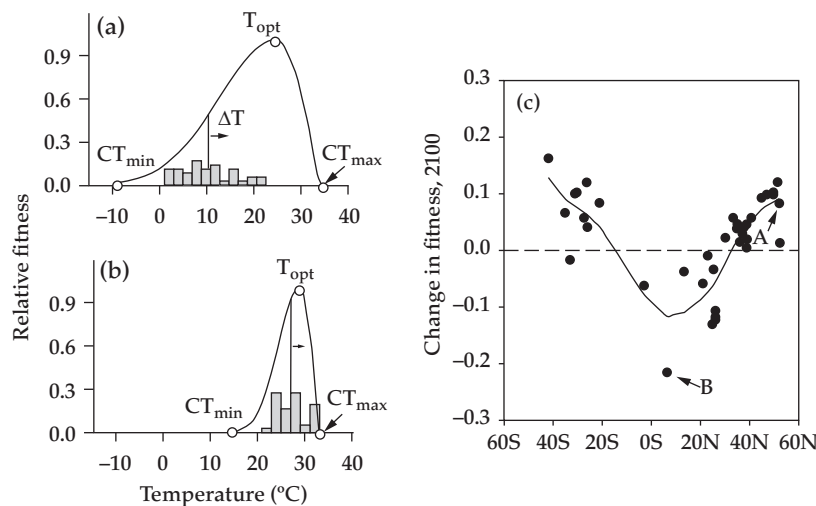


Figure 16.5 Fitness curves for representative insect taxa from temperate (a) and tropical (b) locations, and (c) the estimated change in fitness because of climate warming for all insect species studied, as a function of latitude. Fitness curves were derived from measured intrinsic population growth rates versus temperature for 38 species, including *Acyrtosiphon pisum* (Hemiptera) from 52°N (England) (a), and *Clavigralla shadabi* (Hemiptera) from 6°N (Benin) (b). CT_{min} , ΔT , T_{opt} , and CT_{max} are indicated on each curve. Climatological mean annual temperature from 1950–1990 (ΔT , drop lines from each curve), its seasonal and diurnal variation (grey histogram), and its projected increase because of warming in the next century (ΔT , arrows) are shown for the collection location of each species. In (c), negative values indicate decreased rates of population growth in 2100 AD and are found mainly in the tropics. Positive values are found in mid- and high-latitudes. Modified from Deutsch et al. (2008); (c) (2008) National Academy of Sciences, USA.

ological limits imposed by seasonal energetic bottlenecks (Humphries et al. 2002).

16.4 Conclusions

Environmental change is occurring at an unprecedented rate across the globe. These changes are expected to cause a mismatch between the current phenotypes of populations and the phenotypes best suited for the new conditions. This mismatch can cause decreased fitness and declines in population size that might lead to extirpation and extinction. If populations are to reverse these declines, they will need to reduce the mismatch through immediate behavioural responses, phenotypic (developmental) plasticity, or evolution. Empirical studies of populations in altered environments have documented each of these types of phenotypic change, although it has been difficult to confirm the contribution of evolution in certain scenarios, such as climate change. Moreover, the consequences of adaptive trait evolution for population size and persistence are unknown in natural populations.

Theoretical conditions do exist under which adaptive evolution makes the difference between population persistence versus extirpation, but no studies of natural populations have tested the resulting predictions—and only a few have done so in the laboratory. In general, it is expected that adaptation to new conditions will often, although not always, be fuelled by standing genetic variation rather than new mutations. In either case, this adaptation can involve a few genes of large effect all the way through to many genes of minor effect—or different combinations thereof. Further studies utilizing new genomic tools in natural populations should help to establish the frequency and relevance of different types of genetic variation in adaptive responses to environmental change. Although evolution will almost certainly be important in mitigating the negative effects of climate change—it is not all powerful. Evolution can be constrained by insufficient genetic variation, correlations between traits under antagonistic selection, or functional/physiological trade-offs or limits.

Overall, our understanding of evolutionary responses to environmental change, and of evolu-

tionary rescue, is rudimentary. In particular, we require an improved understanding of the role of population sizes, gene flow, mutation, the genetic architecture of relevant traits, trade-offs, and physiological limits. And it seems likely that the greatest advances will be made through the integration of different research approaches that target several functional and biological levels (e.g. mutations, genes, phenotypes, individuals, fitness, populations, communities, ecosystems). As this knowledge grows, it should improve our ability to predict evolutionary responses to climate change—and the resulting consequences of biological diversity.

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