

## **Patterns of biodiversity and limits to adaptation in time and space**

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## **Abstract**

Species replace each other in space and time because a single species cannot adapt to all environments. Failure to adapt to a changing environment in time leads to extinction, while failure to adapt to a changing environment in space generates the finite ranges that are a feature of all species. Understanding patterns of biodiversity therefore depends on understanding what limits adaptation to ecological change both at range margins, and in all populations over time. Here, we review theoretical models and empirical data concerning what determines maximum rates of adaptation in time or in space, and try to draw parallels between them. The key issues for both types of model are the amount of additive genetic variation available in the direction demanded by selection, which may be low even if variation in single traits is high, and the demographic costs incurred by populations while they adapt to changing optima. Not only is measurement of these parameters data and labour intensive, they are also likely to vary from population to population and generation to generation, even for a single species. For this reason, it remains difficult to predict how easily, or how rapidly, evolution will occur in response to ecological change in a given situation.

## **Why do species have finite ranges in space and time?**

All species have limited ecological distributions, and all species eventually become extinct. At the heart of these distributional limits is the idea of trade offs: a single population or species cannot maximise its fitness in all environments (Woodward and Kelly, 2003). Each species therefore occupies a limited range of ecological conditions, or a particular period in history, and interacts in highly complex ways in ecosystems consisting of many co-existing species. The complexity of these interactions may in turn generate more specialisation (Schemske, this volume; Nosil and Harmon, this volume). However, from an evolutionary biology perspective this explanation is incomplete. Populations clearly adapt to novel environments in some circumstances, otherwise there would be no life on land, and no mammals in the ocean, and only a very few species on oceanic islands such as Hawaii (Wagner and Funk, 1995). What processes therefore act to constrain adaptation to changing environments, and continually prevent the expansion of species into new habitats at the edge of their range?

Understanding the factors that limit the temporal or spatial persistence of species is of key practical importance, given ongoing changes in global climate (Root *et al.* 2003), coupled with rapid habitat loss and alteration by the introduction of exotic species of parasites, predators and competitors. Models based on species' existing ecological tolerances estimate that at least 11% of species will become extinct this century due to climate change alone, even if populations can freely disperse to track the distribution of suitable habitat (Thomas *et al.* 2004; see Parmesan, 2006). This figure will be an

underestimate where dispersal is limited, or if local adaptation already exists within a species' range, meaning that ecological tolerances of single populations are actually lower than models assume (Harte *et al.* 2004). Conversely, extinction rates will be reduced if species can rapidly evolve to changing conditions, allowing the exploitation of more widespread habitats, and reducing the necessity for the large geographical range shifts (Schwartz *et al.* 2006; Bridle and Vines 2007). These issues bring together the issue of limits to adaptation in time as well as in space: why should populations respond to changes in their environments over time if they are consistently unable to respond to spatially variable selection, as demonstrated by their current stable margins? Is adaptation within populations over time easier than for populations distributed across an ecological gradient? Alternatively, are ecological limits to species' distributions only stable over short evolutionary time scales?

In this chapter we review theoretical models for limits to the response of populations to temporal or spatial changes in selection. We then consider how these models are connected theoretically, and briefly review empirical data relating to the critical issues raised by these models. Finally, we ask how relevant limits to adaptation are to existing patterns of biodiversity, and highlight key areas for future research.

### **Limits to adaptation in time: the cost of shifting optima**

For quantitative traits determined by more than a few loci, evolutionary change can be summarised by changes in the mean and the variance of a trait, or its covariance with

other traits. The rate of adaptation of this trait is determined by the amount of additive genetic variance in fitness (Fisher, 1930). However, this genetic variance in fitness comes at a cost, because it means that not all individuals match local optima. The continual loss of productivity due to genetic variance in fitness is termed the “standing load” of a population, and is due to segregation, recombination and stabilising selection around an optimum (Haldane, 1957). Should the selective optimum change, the response of a population to directional selection generates a substitution load (the “cost of selection”), which can be defined as the number of selective deaths required to generate a given change in trait mean (Haldane, 1957; Barton and Partridge, 2000; Figure 1). However, while the population responds to this shifting optimum, there is also a third type of load (the “lag load” or “evolutionary load”), which is the fitness cost of the population remaining a given distance from the local selective optimum (Lande, 1976). The magnitude of this lag, relative to the width of the stabilising selection function (a measure of the strength of selection), determines the mean fitness of the population and therefore its growth rate, so reducing population density. Above a critical rate of environmental change, the lag load becomes so great that it matches the population’s rate of growth, and extinction occurs.

Following the model presented by Lande (1976), Lynch and Lande (1993) considered the relationship between the rate of environmental change in time and extinction using a deterministic model of weak stabilising selection towards an optimal phenotype. Lynch and Lande (1993) found that the upper bound to where the population has zero growth ( $k'_c$ ) is given by  $k'_c < V_G \sqrt{2\bar{r}_{\max}} / V_S$ , where  $V_G$  is the genetic variance,  $V_S$  is the width of

the stabilising selection function and  $\bar{r}_{\max} = r_{\max} - \frac{V_P}{2V_S}$  is the maximum rate of population increase when the population mean trait is at the optimum. Generally speaking, these models suggest that the lag of the trait mean behind a smoothly changing optimum is the key issue determining the upper rate of ecological change that can be matched by evolutionary change without causing the population's extinction. The magnitude of this lag is proportional to the speed of movement of the optimum times the strength of stabilising selection, divided by the square of genetic variance. For a smooth, directional change in the environment, increasing genetic variation increases the maximum rate of evolution, thus reducing the lag load (Figure 2). Similarly, the lag load decreases with the strength of selection, but the optimal genetic variance (when the population grows the fastest) increases with the strength of selection. This is because although for a given genetic variance, stronger selection increases the per generation standing load of genetic variation, this effect is more than counterbalanced by its effect in causing the population to track the shifting optimum more closely, so reducing the total size of the lag load.

Lande and Shannon (1996) explored how the pattern of environmental change affects maximum adaptive rates by contrasting smoothly changing environments with cyclic or randomly changing environments, and considering the effect of genetic variance on population persistence in each case. They concluded that increased genetic variance does not always enhance the probability of survival. Instead, the value of genetic variance depends on the pattern of environmental change, and its effect of reducing evolutionary load overall must be compared with the selective cost of genetic variation per generation. Where changes in the environment are predictable, but fluctuate in a cyclic or

autocorrelated fashion, increased genetic variation only increases adaptability if the period of environmental change is much longer than the generation time, and if the magnitude of the oscillations is sufficiently large that the increased rate of evolution outweighs the per generation cost of genetic variation. Genetic variance is therefore a benefit where the population is often far from its optimum (and selection is sufficiently strong), but is a cost where the optimum changes too quickly for increased evolutionary rates to be an important advantage. These results highlight how the evolutionary responses of populations critically depend on the temporal pattern of environmental change. Similar conclusions were obtained by Charlesworth (1993a, b) and also by Bürger (1999) and Waxman and Peck (1999) in reference to the evolution of genetic variance in changing environments.

Bürger and Lynch (1995) extended Lynch and Lande's (1993) model to include genetic and demographic stochasticity by sampling individuals at random to found the next generation of parents, whenever the population size was greater than the population's carrying capacity given its trait mean. They estimate that demographic and genetic stochasticity alone can reduce the critical rate of environmental change to only 1% of the phenotypic standard deviation per generation (an order of magnitude less than the deterministic models described above). Stochasticity raises the probability of extinction because even though it occasionally boosts the mean phenotype towards the optimum, the negative consequences of moving the population away from, or overshooting, the optimum more than outweigh this effect. In addition, genetic variance can change substantially from generation to generation, and may take several generations to recover

from periods of low variation. By contrast, high levels of genetic variance are removed by only a single generation of low population size. Importantly, Burger and Lynch (1995) find that increasing initial population size only reduces the probability of extinction when the rate of environmental change is relatively low. This is because the amount of genetic variance rapidly levels off with increasing population size, so that with high rates of environmental change, even very large populations will rapidly become extinct.

Another class of models deals with how populations adapt to abrupt rather than gradual environmental change. Gomulkiewicz and Holt (1995) examine a population that is shrinking after a sudden change in the environment, and ask whether adaptation can restore a positive growth rate before the population becomes too small to avoid extinction through demographic stochasticity. They find that only large populations with high levels of additive genetic variance in fitness are likely to be rescued from extinction by adaptation, and then only if the initial change in the environment is small relative to the standing phenotypic variation.

As well as generating increased lag load, a greater proportion of mutations is favourable the further the population is from the selective optimum, including those of large phenotypic effect (Fisher, 1930; Poon and Otto 2000; Orr, 2005; Martins and Lenormand, 2006, Kopp and Hermisson 2007). This phenomenon may allow adaptation to occur at a faster rate than predicted by deterministic models. For example, individual-based simulation models developed by Boulding and Hay (2001) found that adaptation was possible even when the population mean was shifted more than two phenotypic standard

deviations from the optimum. This was because, rather than assuming a fixed variance scaled according to the mean, adaptation could occur by the spread of rare, extremely beneficial genotypes provided the population's growth rate was high, and the starting population size large. However, the maladapted population must persist for sufficiently long for such highly beneficial, multilocus genotypes to arise. The relative importance of novel mutations of large effect on maximum rates of adaptation in natural populations remains an open question.

### **Limits to adaptation in space**

As selection changes in time within populations, it also varies across a species' geographical range. Where species show clinal divergence throughout their range, migration along the spatial selective gradient will act to increase genetic variance in fitness above the expectations of single population models (Felsenstein, 1976; Wilson and Turelli, 1986; Lenormand, 2002). In particular, for marginal populations, genetic variance will be dominated by the effects of gene flow rather than local population size. This "spreading" effect increases the evolutionary capacity of the population to adapt towards the environmental optimum (Slatkin and Maruyama 1975; Gomulkiewicz *et al* 1999; Alleaume-Benharira *et al.* 2006; Bolnick and Nosil, 2007), as well as potentially rescuing the population from extinction by continually introducing new individuals to the margins (Holt, 2003). However, at the same time, immigration from differently-adapted populations displaces the population phenotypic mean away from the local optimum (a "migration load" in this case, analogous to the lag load discussed above), reducing

population growth and therefore reducing population density (a “swamping” rather than “spreading” effect of gene flow). Migration also maintains high levels of “standing load” because genetic variance remains high, even when the mean matches the optimum.

It has been shown by Slatkin (1973) and Nagylaki (1975), that divergence is only possible if the environment changes over a scale which is large enough relative to the ratio of dispersal over the square root of intensity of selection per gene,  $\sigma/\sqrt{s}$ . If environment changes only over smaller scales, a cline in allele frequency cannot develop. Instead, the gene frequencies respond to the selection averaged over the characteristic length. It follows from the more general treatment of Nagylaki (1975) that adaptation to habitats smaller than about  $\sigma/\sqrt{s}$  is prevented if the difference in the ratio of selection coefficients over the characteristic length is large. In the following section, we deal with environments that are gradually changing on habitats much larger than  $\sigma/\sqrt{s}$ .

In the simplest models of evolution at range margins, beginning with Haldane’s theory of a cline (1956), and developed by Pease et al. (1989) and Kirkpatrick and Barton (1997), a continuous population persists along a selective gradient that varies smoothly in space (Figure 3). Evolution is modelled by changes in the mean of a trait to match this selective gradient. As with models for selection in time, population growth rate is a function of how closely the trait matches the environmental optimum at that point on the gradient. When the population is able to track the optimum, the species can expand along the gradient and density remains high (Figure 3a). However, if the selective gradient is too steep relative to the amount of genetic variation available, the population declines in

mean fitness at a rate proportional to the distance of the trait mean from the optimum. Migration now comes mainly from the central, well-adapted parts of the range into the margins, meaning that marginal populations remain distant from the local selective optimum (Figure 3b). In such models, where gene flow is biased towards the influx of genes into marginal populations, adaptation is effectively biased towards those environmental conditions where the largest number of individuals persist (Holt and Gaines, 1992; Kawecki and Holt, 2002).

The Kirkpatrick and Barton (1997) model focuses on the swamping consequence of gene flow, and predicts that adaptation at range margins is determined by the steepness of a selective gradient, or the amount of gene flow along it (defined as the “rate of change in selection”), relative to the amount of genetic variation in fitness available (Figure 4). Species’ margins should therefore be associated with locally steep selective gradients and/or areas where gene flow is locally increased. The restriction of gene flow along selective gradients (by the evolution of assortative mating or habitat choice) may therefore be necessary for adaptive radiation into novel environments.

Although increasing genetic variation throughout the range increased the maximum rate of change a population could adapt to (Figure 4), Kirkpatrick and Barton (1997) did not allow genetic variance within populations to be elevated by migration along the environmental gradient. Barton (2001) extended the Kirkpatrick and Barton (1997) model to allow the evolution of genetic variance, and found that, for a range of plausible genetic models, the swamping effect of gene flow was outweighed by the associated increase in

genetic variance. This allowed the population to match the phenotypic optimum, even along very steep selective gradients. However, as with models for selection in time, an absolute critical limit is reached. Although gene flow along even very steep selective gradients provides enough variance to match the optimum perfectly, the demographic cost of these high levels of variance eventually reduces the mean fitness sufficiently to cause population extinction. Butlin *et al.* (2003) and Bridle *et al.* (in revision) considered an individual-based simulation model, the assumptions and behaviour of which closely match Barton's (2001) analytical model for weak selection on a quantitative trait. This study allows the consequences of demographic and genetic stochasticity on adaptation in space to be considered in detail. As with selection in time (Burger and Lynch, 1995), the stochasticity created by finite population size generates limits to adaptation at a wider range of parameter values than those predicted by analytical models.

As with models for selection in time, models for evolution along selective gradients in space also suggest that the evolutionary consequences of gene flow vary depending on how close a population is to its trait optimum. When the population is well adapted, the increased variance introduced by gene flow creates a genetic load that reduces population density. By contrast, in marginal habitats, where the trait mean is already far from the optimum, increased variance is a benefit, as some migrant individuals are close enough to the optimum to reproduce, and extend the population into novel habitat. The effect of gene flow at range margins is analogous to the evolution of recombination which is beneficial only when a population does not match the current selective optimum (see Otto and Lenormand, 2002). However, differences are likely in the spatial scale at which the

swamping and spreading effects of gene flow operate across a species' range. Although genetic variance (and evolutionary potential) may be significantly inflated by only small levels of gene flow, the swamping of local adaptation may require higher levels of migration, and may only be important where migration is asymmetrical (Endler, 1973; Felsenstein, 1976; Kawecki and Holt, 2002).

### **Integrating limits to adaptation in time and space**

Limits to the rates of evolution in time and in space are connected, in that both depend on the amount of genetic variance (either dominated by mutation/selection balance, or because of gene flow), and on the demographic cost of being displaced from the selective optimum. The optimum can change over time or vary due to gene flow along a gradient, where selection varies in space. The key question therefore becomes: at what point does the genetic variance (the standing load), or the distance of a population's mean from the optimum (the lag load), have such a high demographic cost that the population goes extinct?

Adapting to environment changing in time or space, in both cases the critical rate of environmental change above which the population goes extinct, or stops adapting to a changing gradient in space is driven by similar equations. Here we present the critical rates of change under joint evolution of trait mean and population density (see Lande 1976, Eq. 7; Lande and Shannon 1996, Eq. 1-3; Kirkpatrick and Barton 1997, Eq. 1 and 7), assuming that density-dependence is "logistic", and that the genetic variance is fixed.

Assessing adaptation in space, migration is approximated by diffusion, with  $\sigma$  as the standard deviation of the migration distance. The population growth rate is then

$$\bar{r} = r_{\max} \left(1 - \frac{n}{K}\right) - \frac{(\bar{z} - \theta)^2}{2V_S} - \frac{V_P}{2V_S},$$

where  $r_{\max}$  is a constant determining maximum growth rate,  $n$  is population density,  $K$  carrying capacity,  $\bar{z}$  is the mean phenotypic value,  $\theta$  is the optimum ( $bx$  at point  $x$  in space, or  $kt$  at point  $t$  in time),  $V_S$  is the width of the stabilising selection, and  $V_P$  the phenotypic variance ( $V_P = V_G + V_E$ , where  $V_E$  is environmental variance). For an optimum changing in time, the maximum sustainable rate of evolution

$$\text{is } k_c = V_G \sqrt{\frac{2\bar{r}_{\max}}{V_S}},$$

which is the same as with no density-dependence (Lynch and Lande 1993).

Considering adaptation in space, the population can adapt on the whole range, adapt only on a limited range, or go extinct from either of those regimes (see Kirkpatrick and Barton, 1997; Barton 2001). First, unless the standing load is too high,  $V_P > 2 r_{\max} V_S$ , the population can adapt with the trait mean matching the environmental gradient ( $b$ ), so

allowing the range to expand without limits. Second, as the gradient steepens above a

critical value,  $b_c \approx \frac{2}{\sigma} \sqrt{\bar{r}_{\max} V_G}$ , the population may fail to adapt. Then the gradient in trait

mean is shallower than the environmental gradient (creating a lag load), and the range is

limited. Although both regimes are locally stable when the space is infinite, boundaries to

the physical space often lead to collapse of the perfect adaptation, resulting in limited

range. The density of a population with a limited range reflects the underlying selective

gradient as the difference between the trait mean and environmental optimum increases

as environmental gradient steepens. Such population becomes extinct throughout the entire range approximately when  $b > \frac{1}{\sigma} \left( \frac{V_G}{\sqrt{V_S}} + 2\bar{r}_{\max} \sqrt{V_S} \right)$  (Kirkpatrick and Barton 1997,

corrected Eq. 16; we assume all genetic variance is additive. Details of the above formulae can be found in Polechová et al., in prep.). When the loss of fitness due to genetic variance as described by  $V_G / (V_S \bar{r}_{\max})$  is large, adaptation fails abruptly at the above threshold: the parameter region, where the solution with limited range exists, tends to zero. Generally, the population is able to adapt to changing conditions if the additive genetic variance and the average growth rate at the optimum  $\bar{r}_{\max} = r_{\max} - \frac{V_P}{2V_S}$  are large.

The ability of the population to adapt in space (as measured by the critical gradient  $b_c$ ) increases with weaker stabilizing selection,  $1/V_S$ . When the optimum changes in time, this is true for  $1/V_S > r_{\max} / V_P$ ; the critical rate of change  $k_c$ , when the population can still persist, decreases again when stabilizing selection is weaker.

Adaptation in space and time are also connected in that the range of ecological conditions that a species experiences while it is adapting to changes in time increases with its range, which is determined by the amount of clinal divergence occurring within a species. A wider range will also typically show larger local population sizes (Gaston, 2000), which is consistent with the predictions of Kirkpatrick and Barton (1997) for the limited range. Larger populations have increased mutational input and can sustain higher demographic cost during adaptation. More widely distributed species should therefore be better at adapting to environmental change over time because their maximum sustainable rate of evolution will be higher. Such species are also more likely to maintain genotypes within

their ranges that are important for adaptation to temporal selective gradients.

Furthermore, populations arrayed across steep selective gradients may be better at evolving to match shifting optima in time, because a given amount of gene flow has a greater effect on genetic variance. There has been only a few attempts to address joint adaptation in space and time: most notably, Pease *et al.* (1989) give predictions for such a scenario, which are valid when the genetic variance is much smaller than the strength of selection. Further models exploring adaptation in environments which vary both in space and time are currently being developed (Polechová *et al.*, in prep.).

### **Predicting maximum rates of adaptation in natural populations**

These theoretical models highlight three key factors that limit the ability of populations to adapt to changing conditions in time or space. For selection in time, such limits result in extinction, whereas for selection in space they result in the distributional limits to species that generate geographical patterns of biodiversity, and determine how species interact in ecological communities. These factors are: (1) The strength of stabilising selection; (2) the rate of change of the selection optima; and (3) the amount of genetic variation in fitness. Below we consider each of these parameters in detail, and briefly summarise the empirical data available.

#### *(1) The strength of selection in natural populations*

The width of the selective function ( $V_S$ ) describes the relative fitness of phenotypes that differ from the optimum for that point on the spatial or temporal selective gradient. A

narrow stabilising selection function increases the standing load due to the existing genetic variance (generated both by mutation and by gene flow from other populations), but for a smoothly changing optimum, strong selection reduces the magnitude of the lag load generated by a given shift in the optimum.

Endler (1986) reviewed selection in natural populations and concluded that strong selection may be quite common. Contemporary studies of adaptive divergence also suggest that substantial changes can occur over short time scales, again implying strong selection (Stockwell *et al.* 2003). However, estimates of the strength of selection using quantitative genetic data vary depending on whether selection is standardised according to the trait mean (Houle, 1992), or according to the trait variance (Lande, 1979; Lande and Arnold, 1983). Standardising by the trait mean estimates the increase in relative fitness for a proportional change in the trait, and generates unrealistically strong estimates of selection (Hereford *et al.* 2004). By contrast, standardising by trait variance estimates the change in relative fitness for change of one standard deviation in a given trait. This more data-intensive method generates estimates of selection that are too weak to have been detected by the sample sizes used in most cases, implying a significant publication bias (Kingsolver *et al.* 2001). In addition, these estimates are typically based on studies of one or two traits, whereas selection will usually act on particular combinations of many traits (Blows, 2007; see below). The likely width of the selective function in nature, and how much it typically varies between traits, populations and species therefore remains uncertain (Hendry, 2005). Estimates of selection also tend to consider a small number of generations, whereas the strength of the selection function may fluctuate substantially

over time, and may be less powerful in the long term than studies of natural and experimental populations suggest. To our knowledge, temporal variation in the strength of selection on a trait is something that has yet to be considered in theoretical models.

*(2) The rate and magnitude of the change in optimum in space and time*

Another key issue in predicting adaptation is the way that the environment changes in time (Felsenstein, 1976; Charlesworth, 1993a,b; Lande and Shannon, 1996; Burger, 1999; Waxman and Peck, 1999), as well in space (Barton, 2001, Case and Taper, 2000; Bridle *et al.*, in revision). This affects both the role of genetic variance, and the effect of the strength of selection on maximum adaptation (Lande and Shannon, 1996; Pease *et al.* 1989).

If defining selective optima is difficult in a single population, then describing how rapidly selective optima change over time or space is much harder. In addition, the rate of change of selection in space is a product not only of the ecological gradient, but also the rate and distance moved by individuals along this gradient (Kirkpatrick and Barton, 1997; Figure 3). The difficulty of estimating spatially-variable selection accurately in the field is compounded by the fact that when we measure clines in quantitative traits we measure the response to selection, not the selective gradient itself, which will almost always be an underestimate (see Case and Taper 2000; Barton, 2001). Conversely, when we measure environmental gradients alone, we are ignoring interactions among different environmental gradients, as well as biotic interactions between species, which may act to locally increase or reduce the selective gradient (Case and Taper, 2000; Case *et al.* 2005).

Such biotic interactions are likely to be important determinants of range margins in many cases (Davis *et al.*, 1998). The nature and magnitude of these interactions can also evolve in response to selection.

There is evidence that species' limits coincide with regions where the environment changes quickly over short distances, rather than being arrayed randomly with respect to the steepness of ecological gradients (Thomas and Kunin, 1999; Gaston, 2000; Parmesan *et al.* 2005). However, the causal importance of ecological or population genetic factors in determining these species limits remains unclear (Roy *et al.* 1998; Holt, 2003; Parmesan *et al.* 2005). In particular, regions of low population density observed where ecological gradients change steeply could be associated either with a lack of suitable genetic variation in fitness, or with high levels of genetic variation resulting from swamping gene flow (Barton, 2001; Butlin *et al.* 2003). Addressing this issue would provide valuable insight into causes of range margins. However, accurately estimating trait means and levels of genetic variation in such situations is challenging because it requires establishing large numbers of laboratory lines from low density populations at species' margins (Bridle *et al.* submitted).

### *(3) The amount of genetic variation in fitness*

As we have seen, the amount of genetic variation in fitness is a key factor affecting maximum rates of adaptation, although its effect depends on the pattern of change in selection (Lande and Shannon, 1996). The rapid responses of small laboratory populations and domesticated organisms to artificial selection suggest that even small populations typically harbour high levels of genetic variation in quantitative traits (Barton and Keightley, 2002). This means that the correlation between population size and genetic variation emphasised by models for adaptation to temporal change may only apply at very low population sizes (Willi *et al.* 2006; Willi *et al.* 2007). Instead, levels of genetic variation may be dominated by gene flow along spatial selective gradients, as emphasised by models for adaptation in space.

Estimates of genetic variance in fitness are the key to estimating maximum evolutionary rates (Fisher, 1930). However, the degree to which genetic variation in single traits relates to actual fitness variation is unclear (Blows and Hoffmann, 2005; Blows, 2007). The critical issue is defining the trait or combination of traits that allows a population to match the local selective optimum (Jones *et al.* 2004; McGuigan, 2006; Hellman and Pineda-Krch, 2007, Blows, 2007). The measurement of single traits is not sufficient, because (i) they are only rarely the sole target of selection and (ii) because divergence in any one trait is constrained by pleiotropy (where each gene affects variation in more than one trait), as well as by linkage disequilibria between loci affecting different traits (Johnson and Barton, 2005). Empirical evidence for constraints resulting in such genetic correlations between traits comes from the very rapid and sustained rates of phenotypic

change generated by artificial selection (where trade-offs can be offset by husbandry) compared with natural selection (Barton and Keightley, 2002). Widespread pleiotropy is also suggested by the high rate of input of mutational variance to quantitative traits relative to the per genome mutational rate (Lynch and Walsh, 1998; chapter 12). Such genetic correlations are likely to increase as organisms become more complex (Fisher 1930; Orr, 2005).

Genetic correlations between traits define “genetic lines of least resistance” (Schluter, 1996, 2000), and may be summarised by the variance-covariance matrix, or G matrix (Lande, 1979, Lande and Arnold, 1983; Houle, 1992; Price *et al.* 1993; Stepan *et al.* 2002). Evolution will be biased in the direction of largest genetic covariance ( $G_{\max}$ ) should the fitness optimum shift, regardless of its actual position relative to the population’s starting point (Figure 5a). Genetic covariance slows the response to selection relative to its maximal rates, as well as significantly increasing the lag load by increasing the number of generations for which the population remains distant from the optimum (Hellmann and Pineda-Krch, 2007). This reduces the maximum sustainable rate of evolution in a way proportional to the difference between the direction of the selective gradient, and the direction of largest genetic covariance (Figure 5b). This effect is increased if the environment fluctuates periodically, rather than changing smoothly over time (Hellman and Pineda-Krch, 2007). Migration between populations diverging in response to spatial selective gradients may also strongly affect the G matrix, potentially constraining evolutionary change more than predicted by single-population models (Guillaume and Whitlock, 2007).

Potentially high levels of covariance among traits led Blows and Hoffmann (2005) to argue that genetic variation in fitness is an important limiting factor in natural populations, despite its abundance in laboratory stocks. For example, Grant and Grant (1995) showed that covariances between traits were more successful than variance in individual traits in predicting the short-term response to natural selection of different beak characters in *Geospiza* finches. Low levels of additive variation in fitness traits also explain the lack of response to selection in *Drosophila birchii* along latitudinal gradients (Hoffmann *et al.* 2003; Kellerman *et al.* 2006). Genetic correlations may also be restricting adaptation to climate change in legumes (Ettersen and Shaw, 2001), as well as the longer-term evolution of fish morphology and *Drosophila* wing shape (McGuigan *et al.* 2006; McGuigan and Blows, 2007). By contrast, McGuigan *et al.* (2005) showed that adaptive divergence within fish species was proportional to genetic variance, rather than being constrained by genetic correlations. Similarly, Caruso *et al.* (2005) suggested that evolutionary change in lobeliads was limited by a lack of genetic variation rather than by genetic correlations *per se*. Such variation between taxa and traits in the importance of genetic correlations to constrain evolutionary rates may reflect increased stability of the G matrix for some traits compared to others, as has been shown theoretically by Jones *et al.* (2003).

Long-term studies of selection in wild populations have provided valuable insight into spatial and temporal variation in selection, and genetic variation in fitness in natural populations. Such studies are especially powerful when coupled with detailed pedigree

information, as in Scottish island populations of Soay Sheep and Red Deer, Great Tits in Oxfordshire, and Collared Flycatchers in Gotland (Qvarnstrom, 1999; Kruuk *et al.* 2001; Merila *et al.* 2001; Sheldon *et al.* 2003; Wilson *et al.* 2006; Garant *et al.* 2007). These studies show that genetic variation in fitness in natural populations is complex, and is often masked by environmental effects on phenotypes, such as condition-dependence and environmental plasticity, particularly where the environment fluctuates substantially between generations. Selection may therefore fail to generate adaptive evolution, despite demonstrably high variation in the reproductive success of phenotypes. Although the weakening of selection on condition-dependent traits reduces the standing load of genetic variance, it is likely to increase both substitutional and lag load. For example, in Red Deer, climatic variation only generates evolutionary change in the small proportion of lineages that already experience favourable ecological conditions (Nussey *et al.* 2005). Substantial evolution may also occur in individual growth rate without being reflected by a change in body size or population mean fitness (Wilson *et al.* 2007). Condition-dependence may therefore reduce maximum sustainable rates of evolution below the estimates of theoretical models.

Alternatively, condition-dependent sexual selection could accelerate the rate of adaptation were females to actively select males closest to the phenotypic optimum, so increasing variation in fitness in the direction required by selection (Lorch *et al.* 2003). At least one experiment provides some support for this idea (Fricke and Arnqvist 2007). However, other studies in *Drosophila* failed to find any effect of sexual selection on adaptation (Holland 2002; Rundle *et al.* 2006), perhaps because intersexual conflict

erased the positive effects of mate choice (Rundle *et al.* 2006), or because very little of the additive variance is in fitness as defined by female choice (Brooks *et al.* 2005; Van Homrigh *et al.* 2007). Also, trade offs between sexual selection and natural selection on secondary sexual characters, such as antler and horn size in Red Deer and Soay Sheep reduce fitness, and may be beneficial in benign years, but costly where competition for food (rather than females) is high (Kruuk *et al.* 2002; Robinson *et al.* 2006). In addition, female choice can only increase adaptation to current rather than future conditions.

Sexual selection will therefore only promote adaptation to temporal ecological change if the optimum changes smoothly over time, rather than fluctuating substantially between generations.

The effects of phenotypic plasticity on rates of adaptation are also complex, and have recently been reviewed by Ghalambor *et al.* (2007). On one hand, plasticity may increase rates of adaptation by allowing populations to persist in novel situations so that selection has time to act. On the other hand plasticity may slow rates of adaptation by reducing the amount of genetic variance exposed to selection in marginal environments.

### **Do limits to adaptation determine species' distributions?**

Evolutionary explanations for distributional limits assume that species are in a quasi-equilibrium state, with their persistence in time or space depending on them tracking environmental change at some sustainable rate. However, limits to adaptation are not the only causes of extinction. For example, extinction may occur when populations lie well

within possible rates of evolution, but adapt successfully to a resource as it becomes increasingly rare or unproductive. Furthermore, some species survive well even when transferred outside their range, at least in the short term (Prince and Carter, 1985). Some European tree species are also still expanding their ranges following post-glacial warming, and so have a more limited geographical distribution than their ecological tolerances suggest (Jump and Penuelas, 2005).

There is a large literature concerning range expansions of organisms during historical climate change, particularly during Quaternary climate change (Hewitt, 1999; Parmesan *et al.* 2005). It is likely that prehistoric range shifts, as well as the persistence *in situ* of trees and herbaceous plant species involved substantial evolutionary change on a timescale comparable with likely rates of ecological change (Davis *et al.* 2005).

However, few data are available concerning what species or populations became extinct during this period, or are of sufficient detail to compare rates of range expansion or adaptation in extant taxa or in different ecological scenarios.

Modern habitat destruction and climate change provide a more direct opportunity to test the importance of evolutionary change in determining the persistence of species in response to rapidly changing ecological conditions. Parmesan and Yohe (2003) analysed data for more than 1700 animal and plant species and showed that 73% have recently shifted their ranges during the latter half of this century (Figure 6a). Similar results are reported by Root *et al.* (2003). These range shifts are similar to those predicted based on the existing ecological tolerances of species, rather than expansion to occupy new

habitats, suggesting that little evolutionary change has occurred over these timescales (Parmesan, 2006). However, more than a quarter of species failed to show evidence for range shifts in response to climate change, particularly at equatorial margins. This observation may reflect rapid adaptation to changing conditions, or may reflect the difficulty of detecting range contractions using species' presence/absence rather than abundance data, or in situations where sampling occurs at large spatial scales (Hill *et al.* 2002). The latter interpretation is supported by Wilson *et al.* (2005) who demonstrated that many butterfly species whose ranges appear static at large spatial scales show rapid and predictable altitudinal range contractions when examined in more detail. However, several of the butterfly species studied still persist at low altitude sites despite significantly increased local temperatures (RJ Wilson and D Gutierrez, pers. comm.), which may reflect rapid adaptation to changing conditions. Similarly rapid evolutionary change has been observed in several species undergoing range expansions at their poleward margins, typically involving increased dispersal (Simmons and Thomas, 2004), shifts in host preference (Thomas *et al.* 2001), or the timing of bud burst or seasonal reproduction (Bradshaw and Holzapfel, 2006). There is also historical and contemporary evidence that some species of small mammals compensate for temperature changes by changes in body size, without showing substantial range shifts (Smith and Betancourt, 1998; Smith *et al.* 1998).

Studies of invasive species also provide an opportunity to test the relative importance of evolutionary change in determining species' distributions. Wiens and Graham (2005) reviewed data for 35 invasive species of reptiles and amphibians, and showed a highly

significant relationship between their northernmost latitudinal limits in their native and introduced ranges (Figure 6b). This suggests that most successful invasive species are pre-adapted to the habitat into which they are successfully introduced. Whether or not a species becomes invasive therefore appears to be largely determined by its existing ecological characteristics rather than by its propensity for evolutionary change.

Studies of current responses to climate change, and contemporary species invasion therefore suggest that limits to adaptation do affect where species are found: most species are shifting their ranges to track the availability to currently suitable habitat, and invasions into novel habitats typically fail. As predicted by theoretical models, ecological change is occurring too rapidly in many cases to allow population persistence *in situ*, meaning that evolutionary change may have little impact on future species' distributions in many cases. However, which of the critical parameters described above is actually preventing evolution in these natural situations? Is there too much, or too little genetic variation? Are population sizes sufficiently large to sustain the genetic load created by shifting optima? Closely-related species showing contrasting responses to ecological change provide invaluable opportunities to test the predictions of theoretical models. Conservation efforts could then focus on managing populations to maintain maximum rates of evolutionary change.

## **Future prospects**

Models exploring the ability of a population to match a shifting optimum in time or space have identified parameter values of particular interest, and provide a robust theoretical framework for testing their relative importance. The problem, however, is that these critical parameters interact in complex ways, and each are difficult to estimate in natural populations. Currently therefore, theoretical models are of limited practical use in predicting maximum rates and spatial scales of evolution in real populations.

If adaptive rates are limited by low levels of genetic variance in fitness due by correlations between traits (Blows and Hoffmann, 2005), rapid evolutionary change may depend on breaking up genetic correlations to allow novel responses to selection. This is supported by evidence for phylogenetic constraints in many taxa, where more closely-related species are more ecologically similar than predicted by chance (Ricklefs and Latham, 1992; Peterson *et al.* 1999; Schluter, 2000). Any changes to the G matrix demanded by ecological change are likely to depend most critically on the spread of new mutations rather than recombination between existing genotypes. For example, gene duplication and sub-functionalisation allows negative pleiotropic interactions to be overcome by the evolution of increased gene number (Otto and Yong, 2002). The emerging discipline of evo-devo, coupled with modern genomic analysis, suggests several promising directions to investigate this in more detail (reviewed by Brakefield *et al.* 2003; Brakefield, 2006; Roff, 2007a,b; Reusch and Wood, 2007), and to explore the distribution of mutational variation available for selection in natural populations (Orr,

2005). In particular, studies of experimental evolution in micro-organisms allow the tracking of novel mutations in situations where the pattern of selective change, gene flow, and recombination can be manipulated and observed over thousands of generations within a single research grant. The integration of such genomic and experimental studies with traditionally distinct population genetic and ecological approaches will allow evaluation of which factors are most crucial in limiting evolutionary responses to ecological change. However, more detailed empirical data are required to relate theoretical models for adaptation to natural situations, and predict how the distributions of species, and interactions between them, will respond to the profound ecological changes that will be a predominant feature of coming centuries.

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## Figure legends

FIGURE 1: Evolutionary load resulting from a changing optimum in time (from Roughgarden, 1979). A) The absolute mean fitness (thick solid line) and the fitness of each genotype through time. The thin solid line represents  $AA$ , the dashed line  $Aa$  and the dotted line  $aa$ . B) Population size (solid line) and the frequency of the  $a$  allele through time. Initially, the population absolute fitness is greater than one and the population is expanding. However, as the environment changes the most common allele ( $A$ ) becomes less fit, but the alternate allele ( $a$ ) is still not fitter than  $A$  and cannot make up for the loss of fitness (Figure 1a). The rate of population expansion declines, and ultimately the population shrinks (Figure 1b). If the fecundity of each genotype is too low, the population goes extinct before  $a$  can fix. The cost of remaining a given distance from the optimum is the lag load. Even if fecundity is moderately high, the load imposed by replacing  $A$  with  $a$  can still cause a dramatic reduction in population size (Figure 1b).

FIGURE 2: Increased genetic variation ( $V_G$ ) reduces genetic load, so increasing the maximum sustainable rate of adaptation for a smooth change in the environment over time ( $k$ ). The curved lines (from left to right) represent lag load  $\frac{k^2 V_S}{2V_G}$  for the rate of change of the optimum  $k = 0.01, 0.1$  and  $0.5$ . The straight line represents standing load  $\frac{V_P}{2V_S}$  with  $V_S$  representing the width of the selective function (a constant in this example), and assuming no environmental effects on phenotypes ( $V_E = 0, V_G = V_P$ ).

FIGURE 3 (a). Range expansion without limit along a one-dimensional selective gradient in space the Kirkpatrick and Barton model (1997). Here, the trait mean (solid line) at each point along the selective gradient matches the environmental optimum (dashed line) everywhere. Population fitness is therefore high, and population size uniformly large (indicated by the size of the circles), and the species continually expands along the gradient. The arrows depict the direction and magnitude of migration between adjacent populations. (b). Range margins generated by migration load in the Kirkpatrick and Barton model (1997) of limits to evolution in space. In this case, the well adapted central population is also the largest, and sends out many migrants to adjacent populations (solid black arrows). These immigrants prevent adjacent populations from reaching their trait optimum (the solid line is displaced from the dashed line), which reduces their fitness and hence their population size. These populations in turn send out migrants that are even less fit, further reducing the fitness and therefore the size of the more peripheral populations. Eventually, the trait mean of the peripheral populations is very far from the optimum, and fitness is so low that population growth is negative even with immigration. Reproduced from Bridle and Vines (2007).

FIGURE 4. Causes of limits to adaptation in space. Plot from Butlin *et al.* (2003), modified from Kirkpatrick and Barton (1997), to show the behaviour of an analytical model exploring adaptation in a fitness trait along a selective gradient. Shading delimits parameter values with different outcomes: Unlimited range (adaptation everywhere); Finite range (adaptation is limited to a region of ecological space); and Extinction (the species is unable to sustain itself along any part of the selective gradient. This model

reveals two parameters to be central to predicting when and where adaptation will occur: (A) The rate of change in the selective optimum and (B) The amount of genetic variation in fitness. The rate of change in the optimum is determined by gene flow as well as local selection (see text for details).

FIGURE 5: Genetic correlations and their effect on lag load. Reproduced from Hellman and Pineda-Krch (2007). (a) The effect of selection on a population some distance from a selective optimum. The variance-covariance ellipse describes the distribution of trait value for traits 1 and 2, and the direction and strength of covariation between them. The fitness peak is represented by concentric circles. The vector  $\beta$  indicates the direction of movement demanded by selection, while  $G_{\max}$  describes the genetic line of least resistance, where genetic variation is maximised. The actual phenotypic change effected ( $\Delta Z$ ) is biased by  $G_{\max}$ . (b). Illustrates how the orientation of these traits affects the magnitude of the lag load for selection on each trait alone, or in combination over time. The population starts on the fitness optimum, which moves at a constant rate per generation (circles). The solid lines indicate the evolutionary response, with dots and circles representing the population mean and the optimum respectively, at 100 generation intervals. The bottom panel shows the lag, or evolutionary load, for each case, which is substantially increased, depending on the orientation of  $G_{\max}$  relative to  $\beta$ .

FIGURE 6: Evidence for niche conservatism: (a) Trends in shifts in species' ranges are on average well predicted by climatic envelope models. Probabilistic models for 677 plant and animal taxa show that most species show changes in distribution that closely

match expectations based on recent climate change (from Parmesan and Yohe, 2003). The black line shows the expected confidence level when best estimates of distributional changes were used, and  $\pi$  (the probability that climate change is the principal cause of biological change) was allowed to vary freely. (b) Highly significant linear regression between the northern range limits for 35 species of reptile and amphibian in their native and introduced ranges (in north America). This suggests that successful invasion depends on preadaptation (from Weins and Graham, 2005). Both of these examples suggest that limits to adaptation significantly affect species' distributions in space and time.

Figure 1

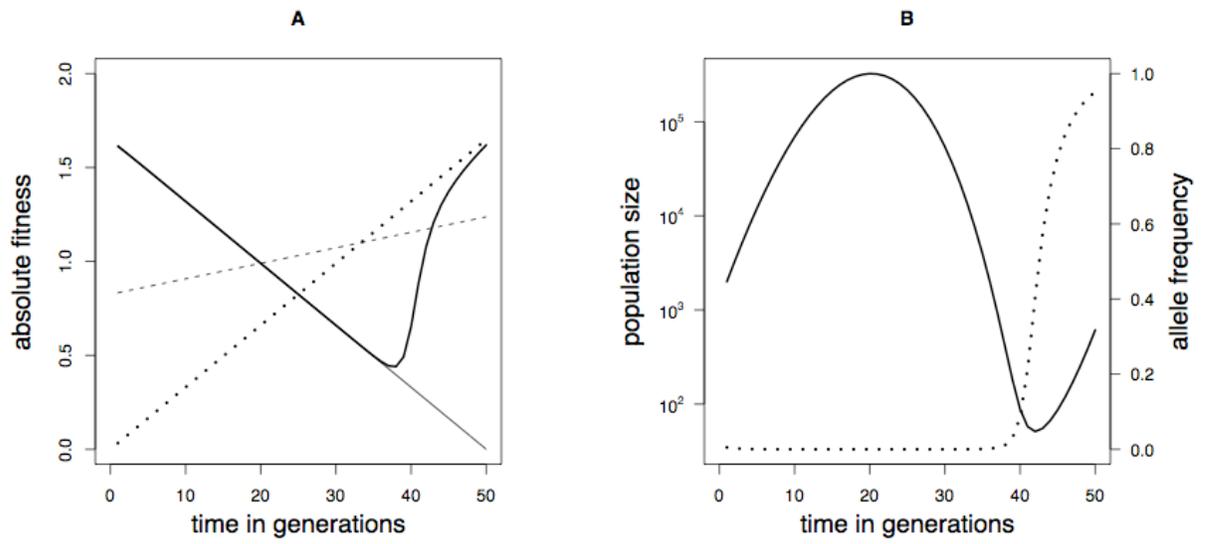


Figure 2

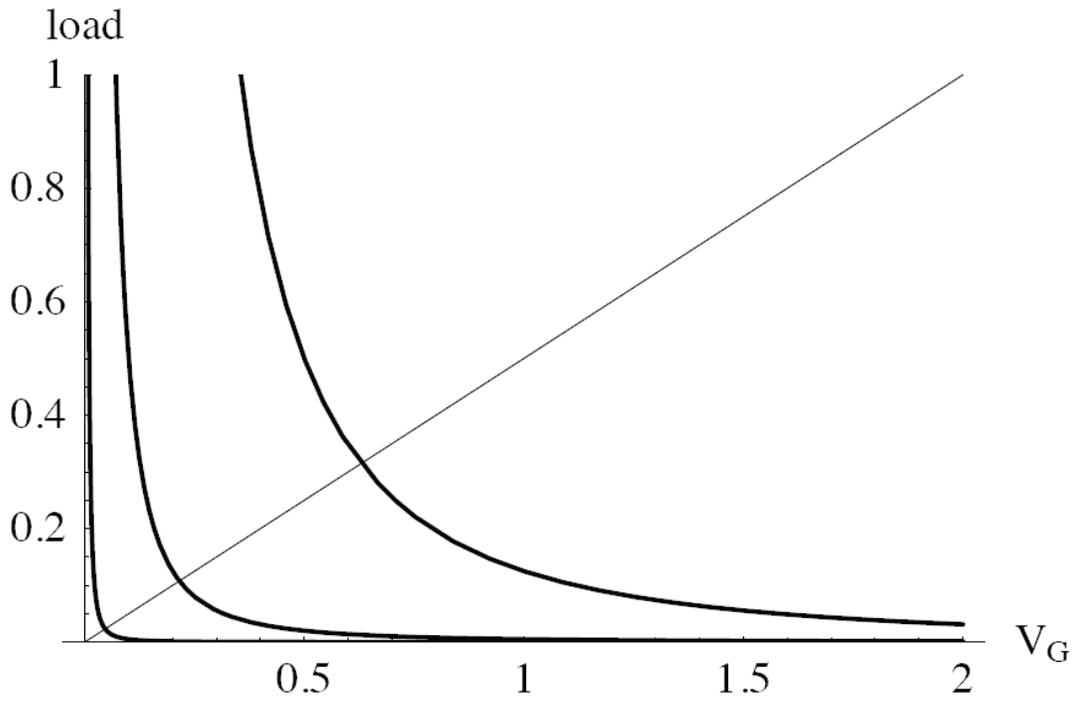


Figure 3

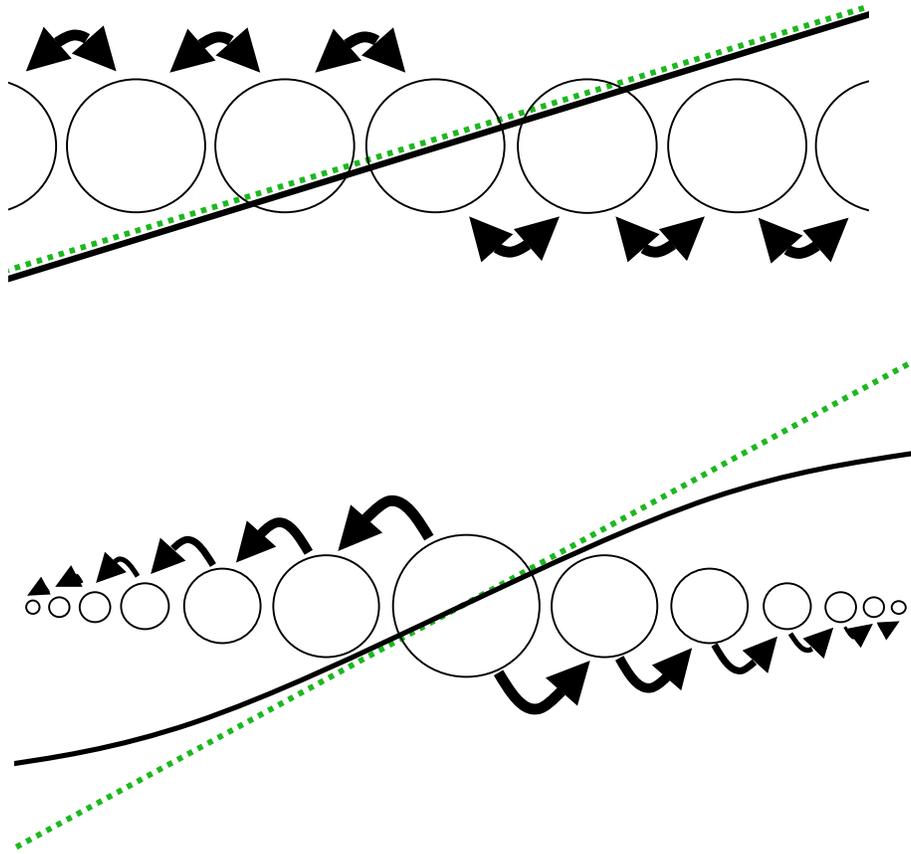


Figure 4

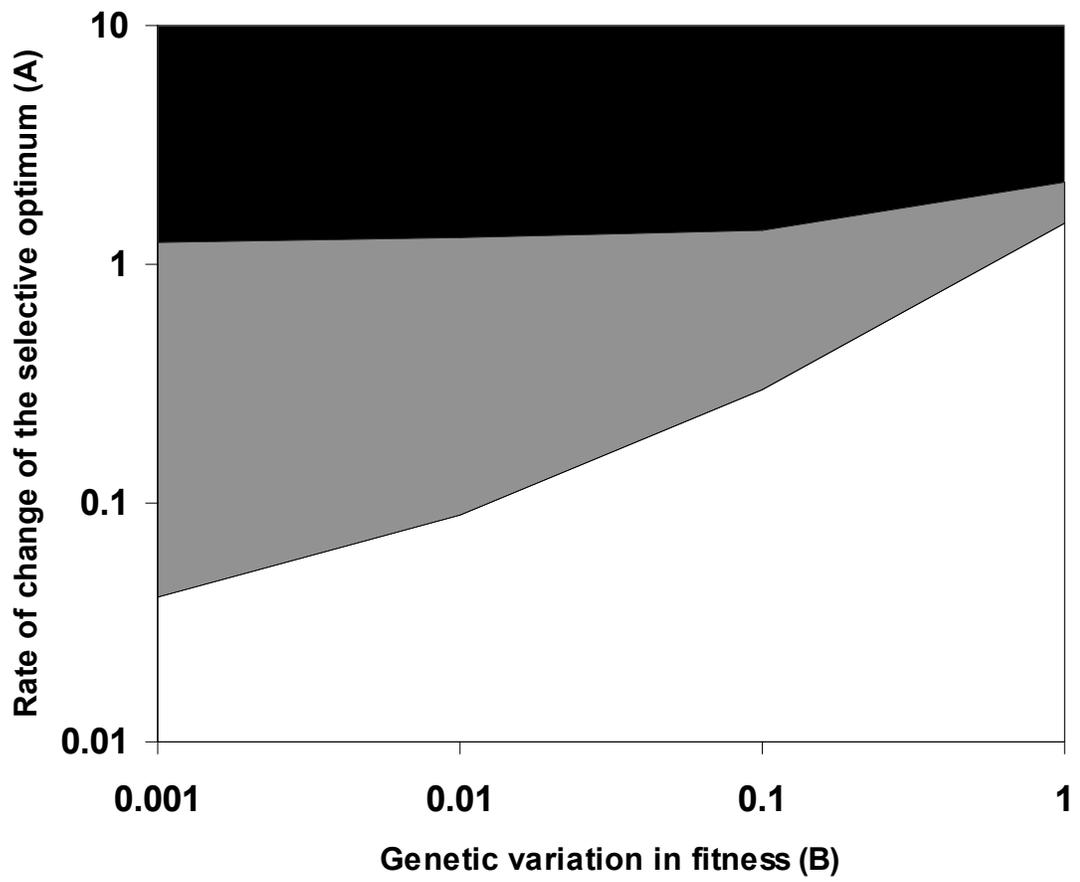


Figure 5a

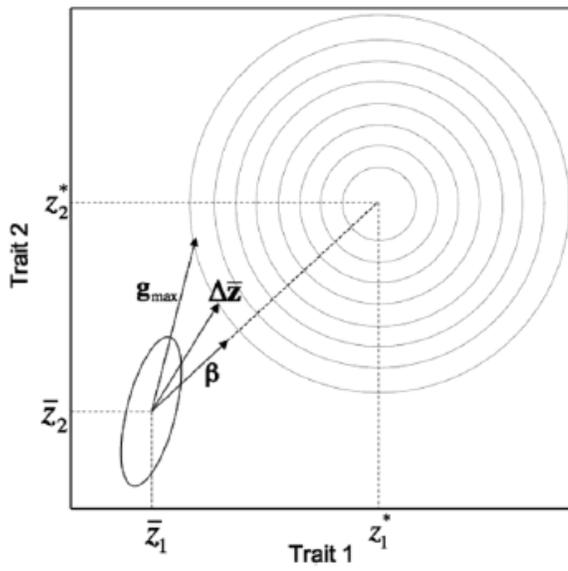


Figure 5b

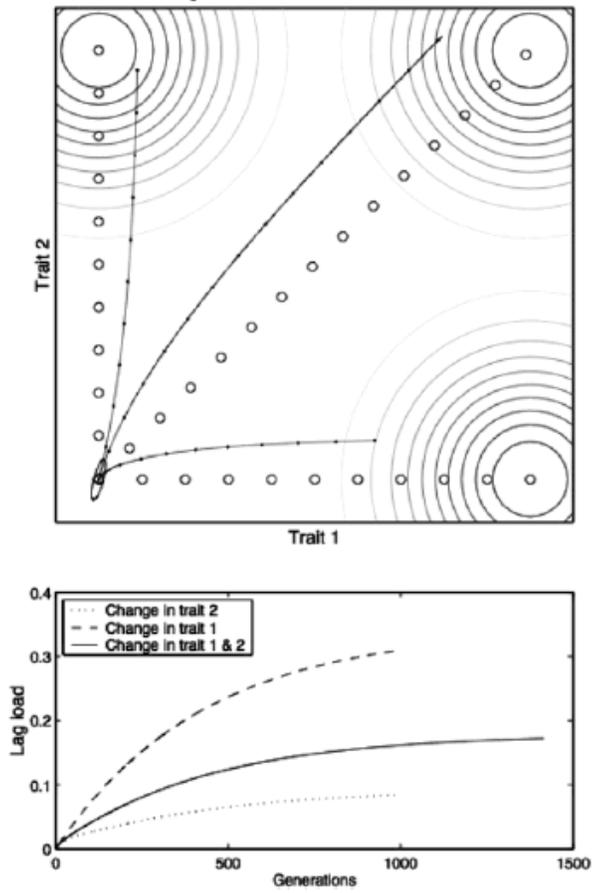
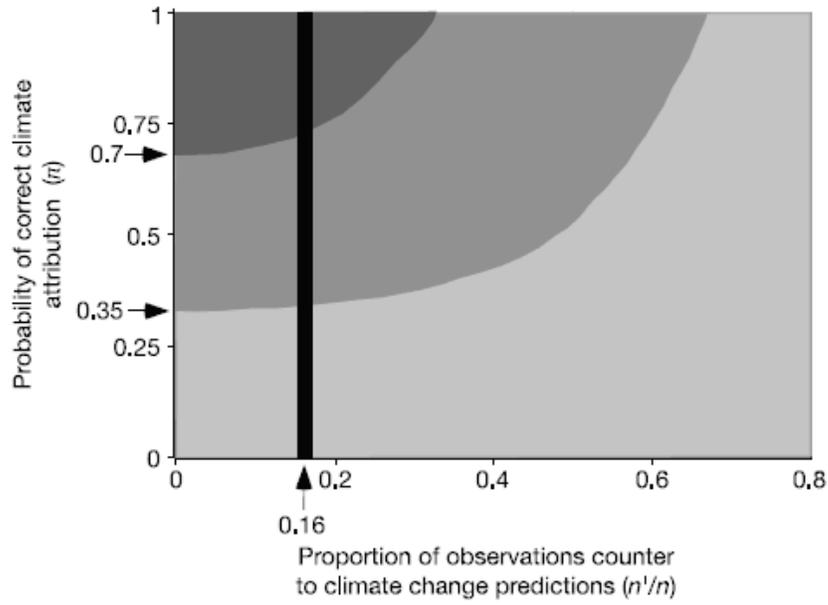
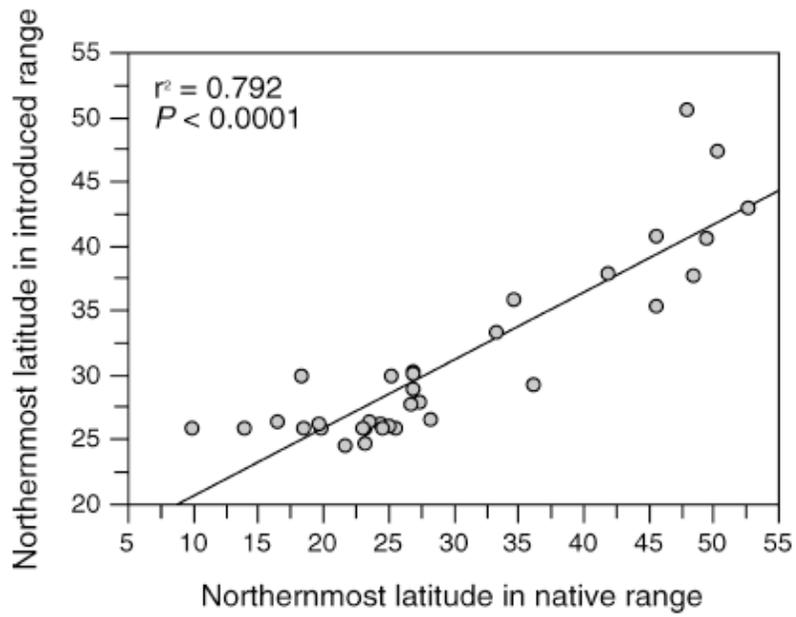


Figure 6

(a)



(b)



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