
III.8

Evolutionary Limits and Constraints

Ary Hoffmann

OUTLINE

1. Lack of genetic variation as a limit and constraint
2. Trade-offs
3. Multivariate selection
4. Gene flow in marginal populations limiting range expansion
5. Limits and constraints: biodiversity and conservation

Although evolution is a powerful process that leads to rapid changes in the characteristics of organisms, limits to evolution arise from a lack of genetic variation, a loss of well-adapted genotypes in populations due to gene flow, trait interactions leading to trade-offs, and/or the difficulty of evolving simultaneous changes in a number of traits. Signatures of genetic constraints at the molecular level include a loss of functional genes as a result of mutational decay.

GLOSSARY

DNA Decay. The loss of functionality of genes as a consequence of mutations and a lack of selection to remove these mutations.

Gene Flow. Movement of genes in space, as a consequence of organisms moving and contributing offspring after they have moved. Gene flow can also occur when gametes move in space (as in movement of pollen).

Genetic Correlation. Effects of the same genetic variants on different traits, as a result of pleiotropy or genetic linkage (tendency for genes to be coinherited because they are located nearby on the same chromosome).

Genetic Variation. Arises because there are different forms (alleles) of the same genes affecting traits. Can be measured by looking for DNA variation in functional genes, variation in their protein products, or

variation in characteristics inherited across generations (*heritability*).

Heritability. The proportion of phenotypic variation in a trait that is controlled by genetic factors (as opposed to environmental factors). Varies from 0 (all variation due to environmental effects) to 1 (all variation due to genetic factors).

Pleiotropy. The multiple characteristics that can be affected by the same genes.

Although evolution can rapidly change the morphology, physiology, and behavior of populations and species, there is also ample evidence that the effects of evolution can be constrained. The fossil record includes many examples of lineages showing long periods of morphological stasis (see chapter VI.11). Some lineages show remarkably little change in appearance across tens or even hundreds of millions of years; cockroaches, the tuatara, cycads, and horseshoe crabs provide a few well-known examples. Such lineages are often considered to have reached an evolutionary dead end, unable to evolve further and constrained to a narrow ecological niche. Yet the effects of selection can be extremely powerful (see chapters III.6 and III.7), perhaps best exemplified by the power of artificial selection in generating crop plants and domesticated animals with little similarity to their wild relatives, and by the rapid adaptation of many species to anthropogenic stresses, such as the development of antibiotic resistance in microbes and pollution/toxin resistance in many invertebrates, fungi, and plants (see chapter III.7); however, even in cases where selection is intense, evolution is not necessarily an inevitable outcome. Although pesticide resistance is widespread in insect pests, weeds, and fungi that cause plant disease, many agricultural chemicals have remained effective against pests for several decades. In these situations the pest populations lack the ability to evolve resistance, evidently because they are constrained in some way.

These types of observations have led evolutionary biologists to search for the reasons underlying constraints. Is it the case that evolutionary change has reached a fundamental limit, unable to occur even when conditions are conducive to adaptation because the set of genetic changes required for adaptation simply are not possible in a species? Or is there some other reason for an evolutionary constraint? A population or species might have the potential to evolve, but other factors like the movement of genes among populations and/or trait interactions make evolutionary change difficult despite ongoing selection. Both fundamental limits and other forms of constraints can prevent populations and species from adapting to new environments. Constraints restrict species to living under a particular set of environmental conditions. In this way, limits and other constraints drive biodiversity; without them, there might be a few common species adapted to a wide range of conditions, rather than a diversity of species, the majority restricted to a narrow range of ecological conditions.

Explanations for evolutionary constraints can be divided into two categories: those that reflect the nature of genetic variation required for evolution and adaptation, and those that have their origin in the ecological processes to which populations and species are exposed.

1. LACK OF GENETIC VARIATION AS A LIMIT AND CONSTRAINT

Natural selection will not change a trait if the trait lacks genetic variation. In the absence of genetic variation, any increase or decrease in the mean value of a trait after selection will not be passed on to the next generation. A way to think about this issue is to imagine a population of individuals derived from a single clone. Barring mutation, all individuals in the population will then be genetically identical, and there will be no genetic variation for any trait in this population. Because of differences in environmental conditions experienced by individuals, they will still differ somewhat in appearance and performance. However, even if these differences affect the fitness of individuals, the differences will not be passed on to subsequent generations because all individuals are genetically identical.

Although natural populations of plants and animals will be genetically diverse rather than derived from a single clone, they may nevertheless have traits lacking genetic variation. One possibility is that populations and species lack specific genes that are required to adapt to new environmental conditions. For instance, Antarctic marine fish have lost the genes coding for proteins and regulatory mechanisms needed to live in warm environments, preventing colonization of warmer waters.

And many species of *Drosophila* vinegar flies lack copies of genes coding for heat shock proteins (HSPs) essential for surviving in hot conditions, where HSPs protect other proteins from degradation. In both these situations, the absence of the appropriate functional genes likely represents a fundamental evolutionary limit. Constraints are also associated with development that influence the body plans and morphological options available to species (see chapters V.11 and V.12).

At the molecular level, this limit can be overcome only by a change in the genome, such as a duplication of another gene or set of genes that evolves a new function and restores the proteins that are required for living in warm water or surviving hot conditions (see chapter V.5). Such changes might then produce an evolutionary lineage consisting of species with the ability to colonize a warmer environment; however, genes are also subjected to DNA decay as mutations accumulate, so they gradually become functionally inactive. DNA decay will occur when there is no selection on a gene to remove mutations that lead to inactivation. The genomes of species contain many genes in a state of decay and on the way to becoming nonfunctional pseudogenes (see chapter V.1). Once DNA decay and eventual gene loss have occurred, function may not easily be restored unless there is a further duplication event and further evolutionary changes to produce a new function.

Because traits are typically affected by a number of genes (and the regulatory mechanisms acting on these genes), genetic variation in a trait may be lost only when there is a cumulative effect of molecular changes at multiple loci, or when a key regulatory gene in a developmental pathway is inactivated. The absence of genetic variation in a trait can be detected through the inability of selection to change the distribution of the trait when artificial or natural selection is imposed in a particular direction (for instance, increased resistance of organisms to warmer or colder conditions, ability of phytophagous insects to use a new host plant, ability of animals to tolerate a disease agent). It can also be detected through a loss of heritable variation (or heritability) in a trait, which is often estimated from family studies (see chapter III.5). Heritability reflects the extent to which variation in a trait is determined by genetic rather than environmental factors, and estimates vary from 0 (all trait variation due to environment rather than genes) to 1 (all variation genetic in origin). A heritability value of 0 points to an evolutionary constraint, resulting in a lack of similarity between parents and their offspring (or between other related individuals). In practice, heritability estimates are prone to large standard errors, meaning that it can be difficult to

distinguish between a low heritability and a true value of 0 that might reflect an evolutionary constraint.

Heritability estimates for morphological traits are typically high in outbreeding species (for instance, estimates for height in populations of domestic animals and humans are often around 0.5 to 0.8), while they tend to be lower for behavioral and physiological traits; however, heritability estimates for natural populations of animals and plants can be quite variable, particularly for traits that are important in determining the ecological niche of species. For instance, the distribution of various *Drosophila* species coincides closely with their levels of resistance to desiccation and cold stresses; species sensitive to cold and dry conditions tend to be confined to moist and warm tropical rain forests, whereas others that are widespread have a high level of resistance to these stresses. Comparisons of heritability for these resistance traits across species indicate that the sensitive tropical species tend toward a very low level of heritable variation (Kellermann et al. 2009). This may help explain why such species are restricted in their distribution—an evolutionary limit exists, based on a lack of genetic variation preventing them moving out of their warm and moist habitats. In a rather different context, Bradshaw and coworkers first found that the limited number of plant species growing on old mine tailings in Europe are the same species that exhibit genetic variation for tolerance of toxic contaminants in soil—these species all contain heritable variation for tolerance in populations not exposed to contaminants. In contrast, plant species that have been unable to evolve and colonize the mine tailings lacked this heritable variation in the first place. These types of cross-species comparisons highlight the potential importance of a lack of genetic variation in limiting evolutionary responses.

As mentioned above, one of the mechanisms likely to drive a loss of genetic variation is DNA decay. When a species becomes restricted to an area because it is dependent on a host plant with a restricted distribution for food or for breeding (as in some birds and phytophagous insects) or because it becomes confined by physical barriers (mountain ranges, water bodies, caves, etc.), there can be a loss of purifying selection for particular characteristics and their underlying genes (e.g., the genes to recognize other host plants and detoxify compounds in them, or to tolerate extremes of temperature). In the absence of purifying selection, the genes will start to undergo decay as they accumulate mutations that may become fixed by genetic drift. Eventually, the decay process will decrease the evolutionary potential of a species should its environment change, perhaps forever confining it to living within a particular set of conditions until a further change in its genome, such as a gene duplication process. It is not clear how often (or how

quickly) DNA decay acts to limit further evolutionary change (or how easy it is for lineages to escape decay).

Another mechanism that can contribute to a loss of genetic variation in traits is strong selection (see chapter III.7). If directional selection for increased expression of a trait persists for many generations, the alleles favored by selection are expected to increase and eventually go to fixation. Once this occurs across all the loci affecting a trait, genetic variation in the trait is expected to decrease toward zero, preventing any further selection response until the strong directional selection is alleviated, and new mutations can accumulate.

2. TRADE-OFFS

While evolutionary constraints due to DNA decay and loss of genetic variation arise because genes are absent and nonfunctional or lack genetic variation, limits can also arise because of the *pleiotropic effects* of genes, which occur when the same genes affect multiple traits. Genes have an enormous potential for pleiotropic effects because proteins encoded by genes are embedded in networks of interacting biochemical processes, and these networks in turn are likely to influence the expression of multiple traits. Moreover, genes that regulate the expression of other genes can have pleiotropic effects by influencing multiple networks. Because of the complex and indirect ways in which genes influence phenotypes (see chapter V.13), selection for a decrease or increase in a trait will favor a set of underlying allelic changes that simultaneously impact other traits.

Genetically based trade-offs occur through pleiotropy when these simultaneous effects influence traits closely related to fitness but in opposing directions. For instance, in insects there is evidence for a genetic trade-off between development time and reproduction, because alleles promoting fast development lead to early emergence and early reproduction by adults, but a cost is paid in that adults emerge at a smaller body size with reduced reproductive output. Similarly, in plants there is evidence for a genetic trade-off between flowering time and seed production, with early-flowering plants tending to produce smaller flowers and potentially less seed. These trade-offs may result in different traits being favored in different environments. For instance, several studies have shown that insect populations living in cool conditions are under strong selection to complete development within a short growing season, resulting in smaller body size and reduced overall reproductive output. Similarly, populations of an invasive wetland plant in cold latitudes have genetically adapted to flower early at the cost of a smaller flower size, compared with populations of the same species in warmer areas (Colautti et al. 2010). In these cases, a

genetically based reduction in reproduction can become an evolutionary constraint if reproductive output is no longer sufficient to sustain a population.

Evolutionary trade-offs can be studied either by considering allelic variants of genes individually or by examining patterns of genetically based correlations among traits. An allele that increases insecticide resistance by boosting a detoxification mechanism will be favored when the chemical is present, but is typically selected against when it is absent, perhaps because the detoxification mechanism is energetically costly. This type of information can point to a mechanistic basis of a trade-off, but might not necessarily provide information about an evolutionary constraint, because other mechanisms of insecticide resistance, such as decreased sensitivity of the target site of the chemical, might be selected instead, and these other mechanisms might not be associated with a trade-off.

For this reason, trade-offs are often characterized by looking at genetic correlations that reflect the effects of the many underlying genes (see chapter III.5). These correlations can be measured through family studies by considering how multiple traits are inherited across generations. Negative genetic correlations for traits affecting fitness in opposing directions, like the association of more rapid development with reduced reproductive output, are then taken as evidence of trade-offs that potentially contribute to evolutionary constraints; however, a negative genetic correlation does not necessarily reflect an evolutionary constraint; unless the negative genetic correlation is particularly strong, the possibility still exists that selection can proceed at least partly independently on the two traits. Some alleles may affect one trait but have no pleiotropic effects on other traits, and might then still be selected. As well as being assessed through family studies, trade-offs can also be investigated by carrying out selection experiments (see chapter III.6), designed to test whether selection on one trait is invariably associated with fitness costs involving a different trait. For instance, many selection experiments in insects, mice, and worms have been undertaken to explore whether an increase in early reproduction is invariably associated with a decrease in longevity as a consequence of allocation of resources to reproduction rather than to maintenance. This trade-off was proposed by George Williams as a way of explaining constraints on the evolution of increasing life span (see chapter III.11 and section VII).

When testing for constraints due to pleiotropy, it is important to distinguish genetic interactions among traits due to chromosomal linkage from those due to pleiotropy. If genes are closely linked along a chromosome, the alleles affecting traits can end up in linkage disequilibrium—an allele that increases development

time might by chance end up linked to an allele affecting reproductive output but from a different, closely linked gene. This issue can be particularly important in selection experiments involving a small number of individuals, with the possibility of strong disequilibrium among loci at the start of the experiment. Although pleiotropic effects can be difficult to distinguish from linkage in practice, linkage associations between traits are expected to be lost as recombination takes place among the linked loci, and so need not impose long-lasting constraints.

Experiments aimed at examining trade-offs and constraints do not necessarily have to involve selection for specific traits, but can also involve the process of *experimental evolution*, whereby populations are held for multiple generations in various environments, to which they usually adapt (see chapter III.6). This approach has been widely used in microbes; for instance, Lenski and colleagues placed *E. coli* bacteria at a temperature of 20 °C, near the lower limit at which these bacteria can be maintained, and monitored adaptation after 2000 generations. They found that the bacterial populations improved in their competitive performance at 20 °C by 8 percent, but at a cost to performance at 40 °C of 20 percent. These findings were interpreted as evidence of trade-offs associated with temperature adaptation; *E. coli* can adapt to low temperatures, but this ability comes at a cost that may constrain evolution in an environment where temperatures are fluctuating.

Although most tests of trade-offs have taken place in experimental laboratory conditions, it is possible to test for the role of trade-offs in generating constraints under field conditions. By crossing a native prairie legume under controlled conditions and then transplanting seed to various locations along a temperature and moisture gradient designed to reflect expected conditions under future climate change, Etterson and Shaw were able to measure natural selection under different field conditions and test for a pattern of genetic correlations among traits related to fitness along the gradient. They showed that because of antagonistic associations among traits, the response to selection along the moisture gradient was expected to be much less than predicted from the heritability of the traits when considered alone. For instance, leaf number was selected to increase where moisture stress occurred, but changes in number were antagonistic to changes in leaf thickness, which was also under selection, constraining the extent to which these traits were expected to change.

Evolutionary constraints due to pleiotropy can be distinguished from those due to a lack of genetic variation by examining the presence of genetic variation in each of the correlated traits. In the former case, each trait is expected to show genetic variation. This situation

applied to most of the traits under selection in the prairie legume studied by Etterson and Shaw. In selection experiments, the persistence of genetic variation in traits even after a selection limit is reached can point to pleiotropy rather than lack of genetic variation acting as an evolutionary constraint.

3. MULTIVARIATE SELECTION

Although trade-offs due to trait interactions are often regarded as essential for evolutionary constraints, other types of genetic interactions among traits can also prevent selection responses. Evolution is constrained when no genetic variation is available for a population to respond in the direction in which selection acts, and this does not necessarily require trade-offs or negative genetic correlations among traits. It is the way in which multiple traits under selection interact at the genetic level that drives eventual selection limits.

Understanding this type of selection limit requires an understanding of selection on multiple traits at once (*multivariate selection* rather than univariate or bivariate selection; see chapter III.4). When a set of traits is under selection, the outcome of selection can be predicted by considering how the traits interact at the genetic level and how selection acts on combinations of traits. As an example of this approach, Blows and colleagues have investigated the cuticular hydrocarbons from males of a *Drosophila* species. The nine different hydrocarbons are under sexual selection caused by female choice, although they are also under natural selection. In family studies, the level of each hydrocarbon shows genetic variation individually, but when considered together the cuticular hydrocarbons show little variation for the specific combination favored by females. In other words, the genetic interactions among the cuticular hydrocarbons prevent much variation from being expressed in the direction favored by sexual selection. In selection experiments, female choice drives only small changes in hydrocarbon profiles before a constraint is reached. Natural selection is also important in determining the hydrocarbon profile of the males, because in selection experiments a change in hydrocarbons due to female choice can be mostly lost when selection is relaxed for a few generations. The evolutionary constraints in this system can therefore really be understood only by considering the ways in which traits are interacting.

4. GENE FLOW IN MARGINAL POPULATIONS LIMITING RANGE EXPANSION

Gene flow occurs when individuals or propagules move from one population to another and then contribute to

the genetic constitution of the other population (see chapter IV.3). This process can both enhance and retard evolutionary adaptation. The former occurs when gene flow increases genetic variation by introducing new genetic variants into a population that can then be selected to increase fitness. On the other hand, when too much gene flow occurs, the effects of selection can be overwhelmed by an influx of nonadapted genotypes. Gene flow can then act as an evolutionary constraint.

The effects of excessive gene flow have been modeled for populations at the geographic margins of species ranges. In some marginal populations, a decreased density of individuals occurs, compared with more centrally located populations. This can result in directional gene flow into the marginal populations, which in some situations may be sufficient to retard adaptation to the conditions experienced by the marginal population. This process might then be sufficient to prevent further expansion of the species.

Although models suggest that directional gene flow can act as a constraint, the empirical data supporting this hypothesis are quite limited. Part of the problem is that marginal populations (particularly for plants) are often just as dense as more centrally located populations, making unidirectional gene flow from high-density central populations to low-density marginal populations unlikely. When gene flow is measured across multiple populations with molecular markers, it often seems to occur in both directions rather than only from central to marginal populations. Perhaps the strongest evidence for this evolutionary constraint comes from transplant experiments suggesting that populations can survive outside their normal range. For instance, annual cocklebur plants moved to north of their range in North America were able to survive and reproduce successfully if induced to reproduce early (Griffiths and Watson 2006), pointing to a role of gene flow in preventing the evolution of early reproduction and subsequent range expansion.

5. LIMITS AND CONSTRAINTS: BIODIVERSITY AND CONSERVATION

Evolutionary constraints are a key determinant of biodiversity. If all species could successfully adapt to changing conditions, it is likely that far fewer species would exist, whereas constraints promote species-level biodiversity. One possible reason tropical areas have a high number of species is that tropical species are more likely to suffer from evolutionary constraints and lack adaptive potential; this seems to be the case for tropical *Drosophila*, which have a low evolutionary potential to adapt to colder and drier conditions when compared to more widespread species. It is possible that many

ecologically specialized species lack adaptive potential because of a low level of genetic variation, or the presence of strong pleiotropic interactions that prevent them from easily adapting, or both. This may, for instance, prevent insect herbivores and parasites from expanding their diets to encompass new hosts, and prevent the spread of species from the humid tropics into drier and cooler climate zones. One possibility is that the processes of DNA decay and mutation accumulation are more likely in some regions—perhaps because species become more easily confined to a narrow-range host plant or because of a geographic barrier. However, it is currently not clear whether particular groups of species from some regions lack adaptive potential, or why this might be the case.

Recognizing adaptive constraints is important for conservation of species and ecological communities, because it can help to identify groups of species at potential risk because of an inability to adapt, or even entire communities if common patterns exist across species groups. Unless they are sufficiently phenotypically plastic (see chapter III.10), these species may be particularly prone to extinction due to disease, climate change, or other stressors. If evolutionary constraints arise because of gene flow, it might be possible to alter levels of gene flow to promote adaptive changes in marginal populations.

Evolutionary constraints are also important from an applied perspective. For instance, when pests and weeds are unable to evolve resistance to pesticides, there is the potential to continue using the pesticides. If the mode of action of pesticides and the genetic basis of resistance are understood, it might be possible to predict the likelihood of resistance developing in a particular evolutionary lineage of pests. On the other hand, where evolution is likely, it may be possible to slow the rate of evolution by ensuring ongoing gene flow between susceptible populations and those under selection. This practice has been adopted in the management of resistance to toxins introduced into crop plants, where resistant crops are interspersed with susceptible cultivars to slow adaptation by pests.

FURTHER READING

Bradshaw, A. D. 1991. The Croonian lecture, 1991: Genostasis and the limits to evolution. *Philosophical Transactions of the*

Royal Society B 333: 289–305. *Outlines the notion of genostasis, in which a lack of genetic variation leads to inability of a species to adapt to stressful conditions, as illustrated by lack of evolutionary ability of many plant species to colonize soil contaminated by mine tailings and other examples.*

Colautti, R. I., C. G. Eckert, and S. C. Barrett. 2010. Evolutionary constraints on adaptive evolution during range expansion in an invasive plant. *Proceedings of the Royal Society B* 277: 1799–1806. *Shows how trait interactions can constrain range expansion during an invasion.*

Connallon, T., and A. G. Clark. 2011. The resolution of sexual antagonism by gene duplication. *Genetics* 187: 919–937. *Indicates how constraints due to antagonistic effects of genes in the different sexes can lead to gene duplication to allow genes to evolve sex-specific functions.*

Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294: 151–154. *Describes an experimental study in which plants were exposed to environmental changes related to climate change and the response to selection was limited by interactions among traits.*

Futuyma, D. J. 2010. Evolutionary constraint and ecological consequence. *Evolution* 64: 1865–1884. *Provides a link between stasis in the fossil record and potential explanations of evolutionary constraints and suggests that microevolutionary constraints may not always be responsible for stasis.*

Kellermann, V., B. Van Heerwaarden, C. M. Sgrò, and A. A. Hoffmann. 2009. Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* 325: 1244–1246. *Outlines an example involving *Drosophila* species in which a lack of genetic variation seems to limit the distribution of species, providing a connection between ecological niches and evolutionary limits.*

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology and Systematics* 40: 415–436. *Provides an overview of ways in which gene flow can limit range expansion at species margins and constrain evolution, with a discussion of empirical studies.*

Walsh, B., and M. W. Blows. 2009. Abundant genetic variation plus strong selection = multivariate genetic constraints: A geometric view of adaptation. *Annual Review of Ecology and Systematics* 40: 41–59. *Outlines ways in which a response to selection can be stopped when genetic interactions occur among traits that constrain the expression of variation in the direction of selection; a very thorough review.*

