

# Ecological Genetics

Mark C Urban, *National Center for Ecological Analysis and Synthesis, Santa Barbara, California, USA*

Ecological genetics is the study of how ecologically relevant traits evolve in natural populations. Early research in ecological genetics demonstrated that natural selection often is strong enough to generate rapid adaptive changes in nature. Modern ecological geneticists combine field observations, laboratory experiments and rapidly improving laboratory techniques to further our understanding about how traits evolve in nature and also to identify which genes are evolving. Ecological geneticists increasingly explore how evolutionary dynamics shape ecological properties. As a consequence, ecological genetics is highly relevant to practical questions that lie at the interface of ecology and evolution.

## Ecological Genetics

Ecological genetics is the study of the evolution of ecologically relevant traits in natural populations (Conner and Hartl, 2004). Ecologically relevant traits are those life history, behavioural, physiological and morphological traits that are related to an individual's fitness or its contribution of offspring to future generations (Via, 1990). The term 'ecological genetics' was coined by the English biologist E. B. Ford (1901–1988) to describe pioneering research on genetic variation in natural populations that combined field observations of natural selection and adaptive trait variation, experimental evolution and laboratory genetics. Early ecological geneticists like Ford worked to overturn the notion, which prevailed at the time, that natural selection was normally too weak to generate substantial adaptive changes in natural populations (Ford, 2005). Indeed, Ford concluded that research in ecological genetics had firmly established that 'unexpectedly great selective forces are normally operating to maintain or to adjust the adaptations of organisms in natural conditions' (Ford, 1964). Today, ecological geneticists continue to advance our understanding of adaptive evolution in natural populations and also apply emerging techniques to reveal the genes underlying important ecological traits and investigate how genetic variation and evolutionary processes shape ecological patterns and processes (Table 1). Hence, ecological genetics is making advances on two fronts by explaining

how species evolve in natural communities and how evolution affects ecological properties such as population abundances and community compositions.

Ecological genetics is nearly synonymous with the field of evolutionary ecology (although the latter is a bit broader) and includes the parts of other subdisciplines such as quantitative and population genetics that apply to adaptive evolution in nature. In general, ecological genetics takes a whole-organism approach to understanding phenotypic evolution, frequently in nonmodel organisms (wild organisms that are difficult to manipulate), and in the process ignores some of the details of the specific changes to deoxyribonucleic acid (DNA) sequences that underlie evolution. This approach can be contrasted with molecular genetics, which focuses on understanding how specific biochemical pathways evolve at the level of nucleic acid substitutions but ignores the details of multitrait phenotypic integration, ecological performance and selection heterogeneity in natural systems. Although the two approaches make simplifying assumptions about evolution, research in ecological and molecular genetics is increasingly integrated, especially as techniques become available to reveal the underlying genetic basis of ecologically relevant traits. The hope is that this integration of molecular and ecological genetics will facilitate progress toward the overarching goal of understanding biology from genes to ecology and back again. **See also:** [Molecular Evolution: Introduction](#)

Evolution in nature can be studied across multiple spatial scales and under differing degrees of ecological complexity. Here I review the practices employed and insights gained by an ecological genetics approach along a continuum of increasing ecological complexity. Because of the interplay between evolution and ecology emphasized by ecological genetics, I explore how environmental and demographic heterogeneity alters phenotypic evolution as well as the converse, how phenotypic evolution alters ecological distributions.

Advanced article

### Article Contents

- Ecological Genetics
- Phenotypic Variation in a Wild Population
- Phenotypic Variation in a Metapopulation
- Multispecies Evolution and Coevolution
- Conclusions
- Biography

Online posting date: 15<sup>th</sup> December 2008

ELS subject area: Ecology

#### How to cite:

Urban, Mark C (December 2008) Ecological Genetics. In: Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd: Chichester.  
DOI: 10.1002/9780470015902.a0021214

**Table 1** Overall objectives and specific questions that can be addressed by the ecological genetics approach

---

The work of ecological geneticists

---

*Overall goals*

Demonstrate and understand adaptive evolution in natural environments

Discover the underlying genetic architecture of ecologically relevant traits

Estimate parameters describing natural selection and genetic variation in the wild

Understand how genetic variation is maintained in the wild

Determine the importance of various constraints and limits to adaptation

Apply ecological questions to pressing social-ecological questions

*Important questions*

*General*

What is the importance of adaptive evolution versus other evolutionary processes?

What is the basis for and consequences of life history tradeoffs?

How does adaptive phenotypic plasticity evolve in variable environments?

How do species and genetic diversity interact to determine ecological and evolutionary rates?

How does phylogeny constrain contemporary community adaptations and ecologies?

*Adaptation over time*

How rapidly can populations respond to temporally fluctuating selection?

What are the implications of adaptation for population persistence in fluctuating environments?

What are the consequences of tightly coupled coevolutionary dynamics?

To what degree is coevolution a pairwise versus a diffuse process?

How do evolutionary dynamics affect population, community and ecosystem dynamics?

*Adaptation in space*

How do traits evolve along environmental clines and other patterns of spatial selection?

How does gene flow alter adaptive evolution?

How does a complex landscape selection mosaic alter coevolutionary dynamics?

How does coevolution affect community interactions across a landscape?

How do colonization/extinction dynamics alter the genetics of interconnected populations?

How does landscape spatial structure affect the evolution of dispersal and habitat selection?

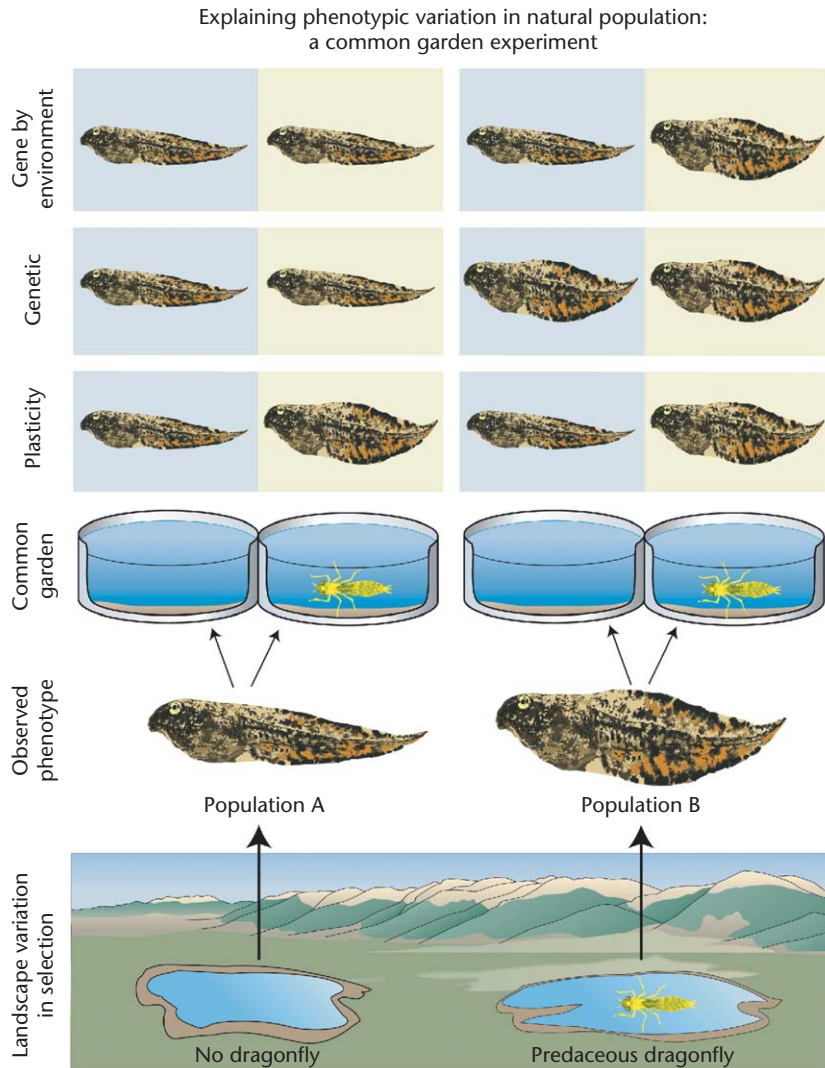
---

## Phenotypic Variation in a Wild Population

In nature, individuals of the same species usually differ in traits such as size, shape, physiology and behaviour both within and between populations. Ecological genetics seeks to explain how and why this phenotypic variation has arisen. By way of example, imagine two tadpole populations, one that lives in a pond inhabited by predaceous dragonflies and another that lives in a predator-free pond (**Figure 1**). Suppose that the tadpoles in the dragonfly pond have deeper tailfins than those in the predator-free pond. At least three reasons can be given for this phenotypic variation, including local adaptation, plasticity and neutral genetic drift. Research in ecological genetics attempts to discern among these and other possible causes of phenotypic variation by integrating research on the spatial and temporal distribution of natural selection (the relationship between a trait value and fitness) and genetic variation in ecologically relevant traits. Whenever possible, phenotypic evolution is studied through experimental manipulations of natural selection or genetic variation in the wild. However, many wild organisms are difficult to manipulate and therefore understanding about their ecological genetics requires a comparative approach in which genetic structure is evaluated across multiple natural populations experiencing varying selection pressures (Via, 1990).

### Local adaptation

The first step toward discerning local adaptations among multiple populations in the comparative approach is to estimate the relationship between the trait of interest and fitness (i.e. natural selection), preferably in the natural environment. The second step is to disentangle genetic from environmental influences on the phenotype. To do this, the phenotypes of individuals are measured in the same environments by transplanting between home and foreign natural environments or under the same carefully controlled artificial conditions called a 'common garden' (see **Figure 1**). Differences that remain among individuals from populations raised in the same environment likely represent variation due to genetic differences (assuming that nongenetically inherited 'maternal effects' can be ignored). The third step is to associate genetically determined trait variation among populations with variation in natural selection regimes, using available insights about the functional performance of traits. For example, suppose that deep tadpole tailfins observed in the population living with dragonflies persisted in a common garden experiment. Moreover, tadpoles with deeper tailfins survived better in the dragonfly pond because their large tailfins allowed them to swim faster and thus escape from dragonflies more often than tadpoles with shallow tailfins. We might then suspect that a deep tailfin is an adaptation to dragonfly predation. An adaptation in this context refers to a



**Figure 1** Ecological geneticists often use common garden experiments to understand the potential determinants of phenotypic variation in natural populations. Here, I assume two populations of tadpoles. Population A lives in a habitat devoid of predators and Population B lives in a habitat with predaceous dragonflies, creating a potential landscape mosaic of heterogeneous selection. The two tadpoles differ in their phenotypes such that the ones living with the predaceous dragonflies have larger tailfins than the other population. A common garden experiment is performed in which eggs from each population are collected from the two natural populations and raised in a controlled environment with and without dragonflies (with each combination replicated many times). Three divergent phenotypic outcomes that might characterize tadpoles raised in the common garden are depicted. If individuals from both populations have bigger tailfins when grown with predaceous dragonflies, but otherwise the populations have similar phenotypes, then nongenetic phenotypic plasticity likely underlies the observed variation. However, if Population B consistently has larger tailfins regardless of treatment and Population A does not (2nd row), then this finding suggests that bigger tailfins might have evolved in Population B. Two caveats are worth mentioning here. First, we would need to confirm that bigger tailfins are associated with higher fitness under attack by predaceous dragonflies through a natural selection experiment. If tailfins do not give rise to higher fitness, they might have evolved due to random drift. Second, maternal effects, the nongenetic inheritance of traits from mothers (e.g. bigger mothers have bigger offspring) could confound results; whenever possible, several generations should be raised in the common garden to eliminate maternal effects. In the topmost row, Population B shows a plastic reaction to dragonflies, whereas Population A does not. This result suggests the evolution of plasticity (a gene by environment interaction) in Population A.

genetically determined phenotype that has evolved in the population because it has higher fitness relative to alternative phenotypes. However, a correlation between genetic variation and environment only suggests the possibility of adaptive evolution. A more powerful approach is to manipulate natural selection in the field and then observe trait evolution

through time (Reznick and Ghalambor, 2005). However, this might not be feasible in some natural systems. **See also:** [Geographical Variation](#); [Natural Selection: Introduction](#)

In addition to studying the causes of phenotypic variation, ecological geneticists also seek to make predictions about future adaptive responses to natural selection. The

breeder's equation from quantitative genetics can be used to predict the genetic response ( $R$ ) to selection:

$$R = h^2 S$$

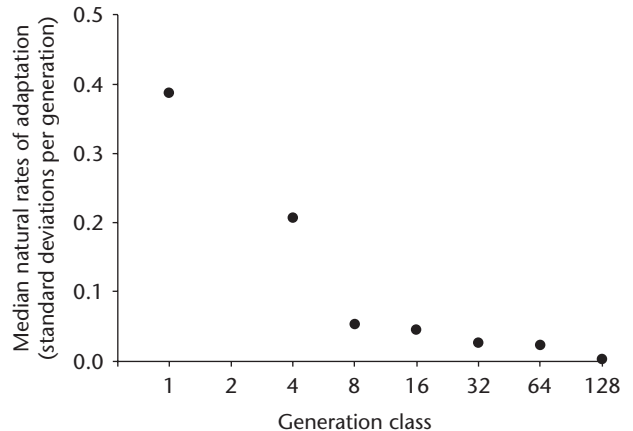
where  $S$  measures selection strength and  $h^2$ , or heritability, measures the proportion of total phenotypic variation that is due to additive (noninteractive) genetic effects. To make these predictions, quantitative genetics approaches are commonly used to estimate the heritability of ecologically relevant traits because these traits are usually underlain by multiple and, as yet, unidentified genes (Via, 1990). An estimated heritability, however, only applies to a specific population, its gene frequencies and the environmental context of measurements (Stearns, 1992). While the breeder's equation offers useful predictions for short-term (5–10 generations) responses to selection, predictions for long-term evolution require a more mechanistic and dynamic understanding of population genetics and natural selection. **See also:** [Quantitative Genetics](#)

Adaptive evolution is certainly not inevitable even under strong selection. Multiple constraints operate at different levels to prevent adaptation (Barton and Partridge, 2000). Physical and chemical laws ultimately circumscribe the realm of phenotypic possibilities. Phylogenetic history limits the range of adaptive novelty in a species because evolution only operates on the raw genetic material passed on by ancestral species. Correlated relationships between genes, their products and their effects on performance make some evolutionary pathways less easily followed than others. Low-fitness valleys can forestall evolution from a local fitness peak to a globally optimal peak by decreasing the fitness of intermediate forms. Also, a simple lack of genetic variation or the swamping of adapted genes by maladapted genes from elsewhere will prevent local adaptation. **See also:** [Adaptation and Constraint: Overview](#)

Despite these constraints, microevolutionary adaptation is common and can occur over just a few generations (Figure 2; Kinnison and Hendry, 2001). This is because natural selection can be strong in nature (Kingsolver *et al.*, 2001) and because significant genetic variation often exists for ecologically relevant traits (Mousseau and Roff, 1987), even though directional selection (when either higher or lower trait values have highest fitness) or stabilizing selection (when an intermediate trait value has highest fitness) can erode this variation. Additive genetic variation is likely maintained in natural populations by temporally varying selection, gene flow, nonadditive interactions among genes, recombination in sexual organisms and mutation. The first two reasons are particularly relevant for natural populations because selection regimes almost always vary markedly in time and space (Endler, 1986).

## Identifying adaptive genes

New and more accessible genetic techniques are making it easier to identify the genes underlying ecologically relevant traits. Quantitative trait locus (QTL) mapping uses recombination patterns between DNA-based genetic markers to



**Figure 2** Adaptive evolution can occur quite quickly, demonstrating substantial changes in trait evolution over the course of just a few generations. Here, the median rates of adaptation (in standard deviations of phenotypic change per generation, the 'Haldane') compiled from published studies are arranged by geometrically distributed bins. Each bin estimates the evolutionary rates from published studies analysed over the number of generations greater than the prior bin up to and including the value of the bin. Note that no data were available for the 1–2 generations bin. Evolutionary rates are high at first but decline when analysed over longer time spans, possibly because optima are quickly reached or because natural selection gradients rapidly reverse, leading to less overall long-term phenotypic change. Data from Kinnison and Hendry (2001).

specify the physical locations of genes that underlie polygenic variation. Microarray methods also can reveal the genes that contribute to divergent phenotypes by allowing comparisons of differential gene expression among individuals. A microarray is a physical grid that contains thousands of DNA probes, each representing a single gene. When a sample of messenger ribonucleic acid (mRNA) from an individual is exposed to the microarray, it binds to probes with matching DNA and fluorescent dyes indicate that a gene has been expressed. At the present time, microarrays have only been developed for a few model species. These genetic tools promise an eventual movement away from the statistical abstraction of quantitative genetics in favour of the precision of population genetics (Conner and Hartl, 2004). However, the wider application of these techniques in ecological genetics awaits their development for nonmodel systems. **See also:** [Microarray Bioinformatics](#); [Quantitative Trait Loci \(QTL\) Mapping](#)

## Phenotypic plasticity

Phenotypic plasticity, or environmentally determined trait expression, often underlies natural phenotypic variation. Therefore, common garden experiments are necessary to tease apart how much phenotypic variation is due to the environment and how much phenotypic variation is due to genetics. Ecological geneticists test for adaptive plasticity by raising close relatives in two or more environments. The resulting trait variation can be partitioned into that due to the environment (plasticity), genes and a gene-by-environment interaction (genetically variable

plasticity). Phenotypic plasticity often enhances an individual's fitness in the environmental context in which it is expressed (Tollrian and Harvell, 1999). For example, large tadpole tails, induced by predaceous dragonflies, can decrease a tadpole's predation risk (Van Buskirk *et al.*, 1997). Phenotypic plasticity, itself, also can evolve in response to local selection. The evolution of phenotypic plasticity requires spatial or temporal heterogeneity in natural selection, predictable selection regimes, and weak fitness costs and genetic limitations to plasticity (DeWitt, 1998; Tollrian and Harvell, 1999). Nevertheless, phenotypic plasticity is common across a range of species and ecosystems, suggesting that these requirements might often be met in nature (Pigliucci, 2001). **See also:** [Environmental Heterogeneity: Temporal and Spatial](#); [Gene–Environment Interaction](#)

## Random drift

Ecological genetics usually focuses on adaptive evolution. However, random drift also can be important in shaping phenotypic variation in natural populations when it overpowers selection on adaptive traits. This is especially true in small populations. Fluctuating selection regimes also lead to periods of neutral fitness and random drift for otherwise adaptive traits. Random drift occurs because underlying alleles are inherited with some random deviance from the frequencies in the last generation. These random deviations become fixed in a population when allele frequencies reach zero or 100%, making further change impossible without mutation or gene flow. Fixation is easier in small populations because there is a greater scope for random deviations (just as a sequence of all 'heads' on a flipped coin is more likely with fewer flips). **See also:** [Drift: Introduction](#)

The persistence of nonadaptive genetic variation in nature can indicate the operation of random drift. For instance, we might suspect random drift if deeper tailed tadpoles were genetically determined, but were equally fit in dragonfly and nondragonfly ponds. However, such conclusions remain speculative until all potentially important agents of natural selection have been measured. Presumed cases of neutral drift are sometimes rejected after new experiments uncover fitness differences among phenotypes (e.g. Schemske and Bierzychudek, 2001).

## Adaptation or drift?

Over the years, substantial effort in ecological genetics has been directed at showing that natural selection can be strong in nature and can generate substantial adaptive differences among wild populations. At the same time, genetic analyses have revealed vast amounts of neutral genetic variation contained in the genomes of organisms. In light of these two pieces of evidence, modern ecological geneticists adopt a pluralistic view of evolutionary biology, which contrasts with the polarized view advanced by the ecological and molecular genetics camps during the 1960s. The current challenge for both ecological and molecular geneticists is to predict the relative importance of adaptive

and neutral microevolutionary processes under varying genetic and ecological contexts.

## Ecological implications of adaptation for population demography

Traditionally, ecological and evolutionary processes were thought to occur at such dramatically different time scales that they could be studied in isolation from each other. However, empirical work has shown that this view is false: evolution can occur at time scales similar to those characterizing ecological changes (Hairston *et al.*, 2005). Thus, ecological and evolutionary dynamics operate over a range of time scales and these time scales frequently overlap. One consequence of this overlap is that natural selection can alter population abundances in different ways, depending on whether selection is hard or soft. Hard selection means that an individual's fitness does not depend on the traits of other individuals in the population. In contrast, under soft selection, an individual's fitness does depend on the traits of other individuals. Selection is considered to be 'soft' in this case because selection can occur with little risk of population extirpation. In hard selection, however, some individuals need to be above the absolute limit imposed by hard selection for the population to persist. Evolution by hard selection still can 'rescue' a declining population as long as evolution increases population fitness above an absolute fitness threshold before the population becomes extinct (Gomulkiewicz and Holt, 1995).

## Phenotypic Variation in a Metapopulation

Few populations are so isolated that we can ignore their connections with nearby populations. The metapopulation, which describes a set of populations linked by migration, acknowledges this natural population structure. The demographic dynamics of the metapopulation are characterized by both migration rates among populations and extinction rates within populations. Many natural populations are thought to behave like metapopulations. Therefore, it is essential that we understand the ecological genetics of the metapopulation. The field of metapopulation genetics accomplishes this objective by exploring how spatial population structure, gene flow and colonization/extinction dynamics shape phenotypic evolution (Hanski and Gaggiotti, 2004). **See also:** [Population Structure](#)

To understand metapopulation genetics, it is important to have accurate estimates of gene flow among populations. Gene flow quantifies the contribution of immigrant genes to a focal population's gene pool and is usually estimated by analysing the spatial structure in neutral genes among populations. Available techniques vary in sophistication, from those that measure simple genetic differentiation (the fixation index,  $F_{st}$ ) to those that incorporate landscape costs to movement. Despite the many approaches, gene

flow continues to be a difficult quantity to pin down with accuracy. To solve this problem, practitioners of the sub-field of landscape genetics are developing better ways of estimating genetic connectivity among populations (Manel *et al.*, 2003). **See also:** [Gene Flow](#), [Haplotype Patterns and Modern Human Origins](#)

## Gene flow-induced phenotypic evolution

Gene flow determines the potential for phenotypic evolution. Without gene flow, local adaptation can be limited because selection only can work on local genetic variation. However, when gene flow is stronger than selection, maladapted genotypes will swamp a local gene pool and prevent adaptation. In this case, all populations adapt to the average or most common selection regime in the metapopulation (Kawecki and Stearns, 1993). Because gene flow and selection usually differ across a landscape, natural populations are generally characterized by varying degrees of adaptation and maladaptation. For example, stickleback fish populations are more or less adapted to lake and stream environments depending on gene flow between the two environments (Hendry and Taylor, 2004).

Adaptive evolution in a metapopulation also can be altered by nonrandom spatial distributions of selection and population size heterogeneity. The more common a selection regime is among neighbouring populations, the more likely those populations will adapt to it (Urban, 2007). Population size asymmetry also can alter adaptive evolution in small populations because a small population will receive more genes from a large population if emigration is proportional to population size. Migrational meltdown occurs when gene flow-induced maladaptation lowers population size and ultimately prevents local adaptation (Ronce and Kirkpatrick, 2001). Lastly, frequent extirpation and recolonization dynamics can generate recurrent founder effects – a local reduction in genetic diversity that results when a few individuals colonize a vacant patch. These founder effects can lead to persistent patterns of reduced genetic variability and low fitness in a metapopulation.

Ecologically relevant traits (those traits that affect an organism's fitness) can be affected by random drift when populations are small and gene flow is low. Only about one migrant per generation is needed to prevent random drift in a population by reintroducing alleles from outside populations that might otherwise become fixed by drift. If drift does occur, it can generate different combinations of randomly fixed alleles in each patch and, as a result, drift homogenizes intra-population genetic variation while accentuating inter-population variation. With higher gene flow, neutral genetic variation depends on dynamics in the metapopulation as a whole, rather than on independent local population dynamics.

## Metapopulation adaptations

A metapopulation perspective forces us to consider natural selection that occurs beyond the boundaries of the local

population. The connectivity, environmental heterogeneity and permanence of populations in a metapopulation can select for traits involved in dispersal. In general, temporal variation in fitness in a patch selects for dispersal because staying can be fatal during bad times. In contrast, spatial variation selects for reduced dispersal because movement can be dangerous and because an emigrant is likely to be maladapted to new environments (Hanski, 1999). 'Spatial selection' also can concentrate the best dispersers in new patches merely because good dispersers arrive first. Thus, young populations will tend to be better dispersers than older populations, which have lost their best dispersers through emigration (Travis and Dytham, 2002).

## Ecological implications of metapopulation genetics

Just as phenotypic evolution can affect population dynamics, phenotypic evolution also can alter metapopulation dynamics. Gene flow can support the so-called genetic rescue effect, whereby adaptive genes arrive from outside sources, counter the negative fitness effects of drift and inbreeding and facilitate local adaptation and population persistence (Tallmon *et al.*, 2004). A population can evolve out of a demographic sink (where local births cannot balance deaths without immigration) when a mutant arrives with an absolute fitness greater than one. When that happens, a sink can become a persistent source population (Holt and Gomulkiewicz, 1997). The evolution of dispersal rate, a so-called metapopulation adaptation, can affect metapopulation dynamics by altering colonization rate (Hanski, 1999). Migrational meltdown, a concept explained previously, offers one explanation for why species range boundaries might remain static through time. If population densities peak in the centre of the range and decline toward the edge of the range, then small edge populations will be so swamped by central genes that they cannot adapt to novel conditions outside the range (Kirkpatrick and Barton, 1997).

## Multispecies Evolution and Coevolution

Here, I consider the evolution of species interactions and the implications of this evolution for community structure. Biotic selection can be quite strong and has likely played an integral role in the macroevolution of species diversity (Thompson, 1999). Many of our best examples of rapid evolution (evolution that occurs on the same time scales as ecological dynamics; Hairston *et al.*, 2005) come from species interactions, including competition between finches (Grant and Grant, 2002), predator–prey dynamics between fish (Reznick *et al.*, 1996) and host–parasite interactions between snails and trematodes (Lively and Dybdahl, 2000). As a result, the evolution of species interactions increasingly is found to affect the composition and

dynamics of natural communities (Whitham *et al.*, 2006; Johnson and Stinchcombe, 2007).

## Coevolutionary dynamics

Coevolution occurs when an agent of selection adapts to the target of its selection. For instance, dragonflies might coevolve with tadpoles if they evolve to swim faster in order to catch tadpoles that had evolved to escape more quickly from dragonflies. Such coadaptations present the opportunity for more interesting evolutionary dynamics than adaptation alone. In character displacement, competition among similar species favours divergent foraging strategies so that the resource-related traits of two competing species diverge more when they co-occur than when they do not (Brown and Wilson, 1956). For example, closely related stickleback fish co-occur in some lakes as two distinct types with morphological adaptations to open-water and benthic food resources (Schluter, 2000). However, nearby lakes are inhabited by a single species with an intermediate foraging morphology that can forage on both resources. Second, frequency-dependent defences and counter-defences in a victim–enemy association can lead to oscillations of allele frequencies and relative fitness through time as both victim and enemy track adaptive changes in each other (e.g. parasites in snails; Dybdahl and Lively, 1998). An enemy–victim arms race is a third possibility, where two interacting species coevolve increasingly effective responses to each other (e.g. toxic newts and toxin-resistant snakes; Brodie *et al.*, 2002). **See also:** [Character Displacement](#); [Inter-specific Coevolution](#)

## Diffuse coevolution

The ecological genetics of coadapted traits generally have focused on strong pairwise interactions. Yet, most species are embedded in multispecies networks of interactions, which creates the potential for many coadaptive relationships. An important question is the degree to which we can understand coevolutionary dynamics as the sum of the fitness effects of multiple pairwise interactions, or if we need to account for the interactive fitness effects among multiple agents of selection (Johnson and Stinchcombe, 2007). Diffuse coevolution characterizes this latter situation because coadaptation between two species is modified by a third species (Strauss and Irwin, 2004). For instance, coevolution between seed-eating crossbills and its food source, lodgepole pines, is altered by the presence of another seed competitor, the red squirrel (Benkman *et al.*, 2003).

## Coevolution in space

Just as we saw for metapopulation genetics, the ecological genetics of species interactions can be shaped by landscape structure. The geographic mosaic theory of coevolution offers three hypotheses about coadaptation across heterogeneous landscapes. Coevolutionary dynamics are expected to be shaped by spatial variation in natural

selection on inter-specific interactions, geographic patterns of reciprocal and nonreciprocal selection termed coevolutionary hotspots and coldspots and trait mixing due to mutation, gene flow, genetic drift and extinction/colonization dynamics (Thompson, 2005). When these conditions are met, the coevolution of species interactions is expected to vary across landscapes. This prediction has been realized for the *Greya politella* moth, which can be a mutualistic pollinator, antagonistic seed parasite or commensal with its flower host depending on the presence of alternative pollinators (Thompson and Cunningham, 2002). **See also:** [Coevolution](#)

## Ecological implications of the evolution of species interactions

The evolution of species interactions can shape emergent ecological patterns such as community diversity, composition and food web structure. Community genetics is a subdiscipline that explores how a genetically variable dominant species affects the dynamics and composition of the species that depend on it (Whitham *et al.*, 2006). For example, cottonwood trees exhibit genetic differentiation in chemical defences against herbivores. As a result, the community of herbivores found on each cottonwood tree differs in a predictable manner depending on host tree genotype. Because evolving species interactions across a landscape can alter community dynamics considerably, ongoing work seeks to unite the views of metapopulation genetics with those of the dynamics of multispecies evolution. For instance, the immigration of maladapted victim species into a community could provide a 'spatial genetic subsidy' to enemy species by providing an easily attacked resource (Urban and Skelly, 2006). In general, the ongoing evolution of interacting species in patches linked together by gene flow is expected to alter local and regional distributions of species abundances and ecosystem properties.

## Conclusions

Ecological genetics bridges ecology and evolution by considering how ecologically relevant traits evolve in nature. The interplay between adaptation, genetic constraints on this adaptation, random drift and gene flow across multiple scales makes ecological genetics both a fascinating and complicated field. Rapidly developing genetic tools increasingly allow us to discover the underlying genetic architecture of ecologically relevant traits. These tools promise to support a much-needed synthesis between ecological and molecular genetics. Ecological geneticists increasingly pursue ecological questions, such as how adaptive trait variation influences population abundances, species interactions and the composition of natural communities. This direct link from evolution to ecology means that ecological genetics is a highly relevant field for solving pressing societal problems. Ecological genetics is currently

being applied to improve agricultural and fisheries production, prevent vector-borne diseases, control invasive species and develop strategies to conserve genetic and species diversity in the face of global anthropogenic disturbances. **See also:** [Adaptations: Meanings](#); [Coevolution](#); [Gene Flow, Haplotype Patterns and Modern Human Origins](#); [Geographical Variation](#); [Microarray Bioinformatics](#); [Population Structure](#)

## Biography

Dr. Mark Urban applies an ecological genetics approach to understand how interacting species evolve across heterogeneous landscapes. His research suggests that adaptations evolve across microgeographic spatial scales as a balance between heterogeneous natural selection and gene flow. His current research focuses on how evolutionary dynamics in species-rich communities connected by gene flow affect emergent ecological properties such as the strength of species interactions, community richness patterns and ecosystem dynamics.

## References

- Barton NH and Partridge L (2000) Limits to natural selection. *BioEssays* **22**: 1075–1084.
- Benkman CW, Parchman TL, Favis A and Siepielski AM (2003) Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. *American Naturalist* **162**: 182–194.
- Brodie ED Jr, Ridenhour BJ and Brodie ED III (2002) The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between garter snakes and newts. *Evolution* **56**: 2067–2082.
- Brown JWL and Wilson EO (1956) Character displacement. *Systematic Zoology* **5**: 49–64.
- Conner JK and Hartl DL (2004) *A Primer of Ecological Genetics*. Sunderland, MA: Sinauer Associates, Inc.
- DeWitt TJ (1998) Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *Journal of Evolutionary Biology* **11**: 465–480.
- Dybdahl MF and Lively CM (1998) Host-parasite coevolution: evidence for rare advantage and time-lagged selection in a natural population. *Evolution* **52**: 1057–1066.
- Endler JA (1986) *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press.
- Ford EB (1964) *Ecological Genetics*. London: Methuen & Co.
- Ford EB (2005) R. A. Fisher: an appreciation. *Genetics* **171**: 415–417.
- Gomulkiewicz R and Holt RD (1995) When does evolution by natural selection prevent extinction? *Evolution* **49**: 201–207.
- Grant PR and Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707–711.
- Hairston NG, Ellner SP, Geber MA, Yoshida T and Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* **8**: 1114–1127.
- Hanski I (1999) *Metapopulation Ecology*. New York: Oxford University Press.
- Hanski I and Gaggiotti OE (2004) *Ecology, Genetics and Evolution of Metapopulations*. Burlington: Elsevier Academic Press.
- Hendry AP and Taylor EB (2004) How much of the variation in adaptive divergence can be explained by gene flow? An evaluation using lake-stream stickleback pairs. *Evolution* **58**: 2319–2331.
- Holt RD and Gomulkiewicz R (1997) How does immigration influence local adaptation? A reexamination of a familiar paradigm. *American Naturalist* **149**: 563–572.
- Johnson MTJ and Stinchcombe JR (2007) An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology & Evolution* **22**: 250–257.
- Kawecki TJ and Stearns SC (1993) The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. *Evolutionary Ecology* **7**: 155–174.
- Kingsolver JG, Hoekstra JE, Hoekstra JM *et al.* (2001) The strength of phenotypic selection in natural populations. *American Naturalist* **157**: 245–261.
- Kinnison MT and Hendry AP (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**: 145–164.
- Kirkpatrick M and Barton NH (1997) Evolution of a species' range. *American Naturalist* **150**: 1–23.
- Lively CM and Dybdahl MF (2000) Parasite adaptation to locally common host genotypes. *Nature* **405**: 679–681.
- Manel S, Schwartz MK, Luikart G and Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution* **18**: 189–197.
- Mousseau TA and Roff DA (1987) Natural selection and the heritability of fitness components. *Heredity* **59**: 181–197.
- Pigliucci M (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, MD: Johns Hopkins University Press.
- Reznick D, Butler MJ, Rodd FH and Ross P (1996) Life history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* **50**: 1651–1660.
- Reznick DN and Ghalambor CK (2005) Selection in nature: experimental manipulations of natural populations. *Integrative and Comparative Biology* **45**: 456–462.
- Ronce O and Kirkpatrick M (2001) When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution* **55**: 1520–1531.
- Schemske DW and Bierzychudek P (2001) Evolution of flower color in the desert annual *Linanthus parryae*: Wright revisited. *Evolution* **55**: 1269–1282.
- Schluter D (2000) *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press.
- Stearns SC (1992) *The Evolution of Life Histories*. New York: Oxford University Press.
- Strauss SY and Irwin RE (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annual Review of Ecology and Systematics* **35**: 435–466.
- Tallmon DA, Luikart G and Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution* **19**: 489–496.
- Thompson JN (1999) The evolution of species interactions. *Science* **284**: 2116–2118.
- Thompson JN (2005) *The Geographic Mosaic of Coevolution*. Chicago: University of Chicago Press.



- Thompson JN and Cunningham BM (2002) Geographic structure and dynamics of coevolutionary selection. *Nature* **417**: 735–738.
- Tollrian R and Harvell CD (1999) *The Ecology and Evolution of Inducible Defenses*. Princeton: Princeton University Press.
- Travis JMJ and Dytham C (2002) Dispersal evolution during invasions. *Evolutionary Ecology Research* **4**: 1119–1129.
- Urban MC (2007) Risky prey behavior evolves in risky habitats. *Proceedings of the National Academy of Sciences of the USA* **104**: 14377–14382.
- Urban MC and Skelly DK (2006) Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* **87**: 1616–1626.
- Van Buskirk J, McCollum SA and Werner EE (1997) Natural selection for environmentally induced phenotypes in tadpoles. *Evolution* **51**: 1983–1992.
- Via S (1990) Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Annual Review of Ecology and Systematics* **35**: 421–446.
- Whitham TG, Bailey JK, Schweitzer JA *et al.* (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews. Genetics* **7**: 510–523.

## Further Reading

- Falconer DS and Mackay TFC (1996) *Introduction to Quantitative Genetics*, 4th edn. Essex, England: Longman.
- Roff DA (2002) *Life History Evolution*. Sunderland, MA: Sinauer Assoc., Inc.