Where does life’s diversity come from? Where do new species come from? Why do some species go extinct?

These are just a few of the questions that can be answered by an understanding of evolution, genetics, and biodiversity. These disciplines explain the mechanisms that shape how organisms interact with their environment and, in turn, how the environment shapes organisms over many generations.

To study ecology without an understanding of evolutionary theory is to watch a sporting event without first learning the rules; players run, points are scored, whistles shrill, but the guiding principles underlying these events remain a mystery. With an understanding of the rules, however, even the smallest intricacies of the game can be appreciated, even loved. So it is with...
Evolution Is Change in the Inherited Traits of a Population through Successive Generations

By: Andrew A. Forbes (Dept. of Biology, University of Iowa) & Billy A. Krimmel (Dept. of Entomology, University of California at Davis) © 2010 Nature Education

Evolution describes changes in inherited traits of populations through successive generations. To fully understand the science of ecology, one must first be able to grasp evolutionary concepts.

The geneticist Theodosius Dobzhansky (1964) famously wrote "nothing in biology makes sense except in the light of evolution," and the field of ecology is no exception to this broadly-embraced principle. To study ecology without an understanding of evolutionary theory is to watch a sporting event without first learning the rules — players run, points are scored, whistles shrill, but the guiding principles underlying these events remain a mystery. With an understanding of the rules, however, even the smallest intricacies of the game can be appreciated, even loved. So it is with ecology: Evolution provides a canon by which we may better understand the interactions of organisms with their environments. In this section, we define evolution as it is understood to modern biology and as it applies to ecology.

Evolution is defined as the change in the inherited traits of a population of organisms through successive generations. When living organisms reproduce, they pass on to their progeny a collection of traits. These traits may be tangible and obvious, such as the patterns in a butterfly’s wing or the number of scales on a crocodile, but they also include characteristics as relatively anonymous as the sequence of nucleotide bases that make up an organism’s DNA. In fact, when we talk about evolutionary inheritance, the latter is what we are actually referring to: the transfer of genetic sequences from one generation to the next. When particular genetic sequences change in a population (e.g., via mutation) and these changes are inherited across successive generations, this is the stuff of evolution.

What Evolution Is Not

The term "evolution" is commonly misused, often accidentally but sometimes with purpose, so it is also necessary to clarify what evolution is not.

Most importantly, evolution does not progress toward an ultimate or proximate goal (Gould 1989). Evolution is not "going somewhere"; it just describes changes in inherited traits over time. Occasionally, and perhaps inevitably, this change results in increases in biological complexity, but to interpret this as "progress" is to misunderstand the mechanism. For instance, that single-celled organisms eventually gave rise to multicellular organisms might appear to exemplify directed movement towards so-called "higher" life-forms. But as Gould (1996) and others point out, there is a left-hand wall to complexity; by definition, the simplest possible organism can only become more complex or stay the same. In this sense, evolution is a "drunkard's walk" (Figure 1), wherein certain lineages inevitably attain unexplored novelty in form and function. By the same token, terms like "reverse evolution" and "devolution" are nonsensical; similar traits and gene sequences may recur at different moments in biological history, but this is still just evolution: change over time.
A second important point is that evolution and natural selection are not equivalent terms. Natural selection is one force that can drive and influence evolutionary change, but other mechanisms can be equally important. Trait changes among the members of a population are not always a result of selective processes. For instance, the appearance and accumulation of a deleterious trait (e.g., a genetic disease) in a population should not be ascribed to direct selection for the trait in question. Similarly, alleles that have no effect on traits under selection may undergo mutations that do not influence the fitness of the organism carrying them. Proponents of the neutral theory of molecular evolution argue that many, if not most, of the genetic differences between species are selectively neutral. What follows is an overview of the variety of forces, including natural selection, that can drive or otherwise influence evolutionary change.

**Microevolution and Macroevolution**

One can distinguish between two general classes of evolutionary change: microevolution (change below the level of the species) and macroevolution (change above the level of the species).

Population ecologists, conservation biologists, and behavioral ecologists are most directly concerned with microevolutionary processes. These include shifts in the values and frequencies of particular traits among members of populations, often due to ecological processes such as the movement of organisms and changing environmental conditions as well as interactions with members of different species (e.g., predator-prey interactions, host-parasite interactions, competition) or the same species (e.g., sexual selection, competition). These processes can, but do not necessarily, lead to the formation of new species over time but instead result in fluctuating frequencies of traits within populations tracking ever-changing selective pressures (Thompson 1998). Since some microevolutionary processes may occur over just a few generations, they can often be observed in nature or in the laboratory.

An appropriate illustration of microevolution in action is the well-documented tendency for insects to rapidly develop resistance to pesticides (Gassmann et al. 2009). For example, during summer in Southern France, pesticides are applied to control *Culex* mosquitoes from the Mediterranean coast to about 20 km inland. Certain mosquito genes confer resistance to the pesticides but are costly in the absence of pesticides (Figure 2): frequencies of the pesticide-resistance gene increase during summers in areas where spraying is common, but do not increase in areas where spraying is not practiced. (Lenormand et al. 1999).
Figure 2: Frequencies of the pesticide-resistance allele Ace.1 in summer (top) and winter (bottom) populations of Culex mosquitoes in coastal France

Pesticides are applied between 0 km and 20 km from the coast during summer months. Coastal frequencies of Ace.1 increase during the summer but then decrease again in the winter.

© 2010 Nature Education All rights reserved.

Usually macroevolutionary changes cannot typically be observed directly because of the large time scales generally involved, though many instances of macroevolutionary change have been observed in the laboratory (Rice & Hostert 1993). Instead, studies of macroevolution tend to rely on inferences from fossil evidence, phylogenetic reconstruction, and extrapolation from microevolutionary patterns. Often the focus of macroevolutionary studies is on speciation: the process by which groups of previously-interbreeding organisms become unable (or unwilling) to successfully mate with each other and produce fertile offspring.

Ecologists may be interested in macroevolution as a means to make inferences regarding present-day ecological questions. Scientists interested in modeling the effects of present-day climate change, for instance, can couple prehistoric climatological data with fossil-derived patterns of speciation and extinction to understand how contemporary animal and plant species are faring today and how they will fare in the future. For example, many marine invertebrates (e.g. corals, snails, clams) construct their shells using calcium carbonate harvested from ocean water. As anthropogenic CO2 accumulates in the atmosphere, a significant fraction of it dissolves into the ocean, releasing free hydrogen ions in the process and thus decreasing oceanic pH. Among other things, this ocean acidification reduces the amount of carbonate available to shell-making marine invertebrates that rely on it for their calcium-carbonate shells, making it difficult for them to make and maintain their shells.

By combining oceanic pH data from hundreds of millions of years ago with fossil records of foraminifera (shell-making marine invertebrates), Zachos et al. (2005) show the effects that ocean acidification have had on the diversification and extinction of past marine invertebrate fauna. From these data, one can model current patterns of ocean acidification and begin to predict its effects on present-day and future marine animals (e.g. Orr et al. 2005).

Conclusion
Evolution describes changes to the inherited traits of organisms across generations. Evolutionary change is not directed towards a goal, nor is it solely dependent on natural selection to shape its path. Ecology, as with any biological discipline, is rooted in evolutionary concepts and best understood in its terms.

References and Recommended Reading


Evolution Is Change in the Inherited Traits of a Population through Successive Generations

The Hardy-Weinberg Principle
Using Molecular Techniques to Answer Ecological Questions
Mutations Are the Raw Materials of Evolution

Avian Egg Coloration and Visual Ecology
The Ecology of Avian Brood Parasitism
The Geography and Ecology of Diversification in Neotropical Freshwaters
The Maintenance of Species Diversity
Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations
Neutral Theory of Species Diversity
Population Genomics
Semelparity and Iteroparity

Explore This Topic

BASIC
Evolution Is Change in the Inherited Traits of a Population through Successive Generations
The Hardy-Weinberg Principle
Using Molecular Techniques to Answer Ecological Questions
Mutations Are the Raw Materials of Evolution

ADVANCED
Avian Egg Coloration and Visual Ecology
The Ecology of Avian Brood Parasitism
The Geography and Ecology of Diversification in Neotropical Freshwaters
The Maintenance of Species Diversity
Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations
Neutral Theory of Species Diversity
Population Genomics
Semelparity and Iteroparity

INTERMEDIATE
Why Are Life Histories So Variable?
Comparative Genomics
Case Study: The Glorious, Golden, and Gigantic Quaking Aspen
Cybertaxonomy and Ecology
Molecular Genetic Techniques and Markers for Ecological Research
Resource Partitioning and Why It Matters

The Hardy-Weinberg Principle

By: Christine A. Andrews (Biological Sciences Collegiate Division, University of Chicago) © 2010 Nature Education


The Hardy-Weinberg theorem characterizes the distributions of genotype frequencies in populations that are not evolving, and is thus the fundamental null model for population genetics.

Basic Mendelian Genetics

Under the now-discredited theory of blending inheritance, the hereditary material was conceived as a fluid that combines the traits from two individuals into phenotypically intermediate offspring. Given observed patterns of resemblance between parents and offspring, blending inheritance may seem intuitively reasonable, as it did to many of Charles Darwin’s contemporaries. This mode of inheritance, however, posed problems for Darwin’s theory of natural selection (1859), which depends on the existence of heritable trait variation in populations of organisms. Blending inheritance would quickly erode such variation, since all traits would be combined from one generation to the next until all individuals shared the same blended phenotype. In his famous experiments on pea plants, Gregor Mendel rejected this hereditary mechanism in favor of particulate inheritance by demonstrating that alternative versions of genes (alleles) account for variations in inherited characters, though he didn’t actually know about genes as such. Although Mendel published his results in 1866, his work remained obscure until its rediscovery in 1900 (reviewed in Monaghan & Corcos 1984), which helped give rise to the modern field of genetics.

Mendel’s Law of Segregation, in modern terms, states that a diploid individual carries two individual copies of each autosomal gene (i.e., one copy on each member of a pair of homologous chromosomes). Each gamete produced by a diploid individual receives only one copy of each gene, which is chosen at random from the two copies found in that individual. Under Mendel’s Law of Segregation, each of the two copies in an individual has an equal chance of being included in a gamete, such that we expect 50% of an individual’s gametes to contain one copy, and 50% to contain the other copy (Figure 1).

Figure 1: Mendel’s Law of Segregation

An individual’s genotype is the combination of alleles found in that individual at a given genetic locus. If there are two alleles in a population at locus A (A and a), then the possible genotypes in that population are AA, Aa, and aa. Individuals with genotype AA are heterozygotes (i.e., they have two different alleles at the A locus). If the heterozygote is phenotypically identical to one of the homozygotes, the allele found in that homozygote is said to be dominant, and the allele found in the other homozygote is recessive.

Even after many geneticists had accepted Mendel’s laws, confusion lingered regarding the maintenance of genetic variation in natural populations. Some opponents of the Mendelian view contended that dominant traits should increase and recessive traits should decrease in frequency, which is not what is observed in real populations. Hardy (1908; Figure 2) refuted such arguments in a paper that, along with an independently published paper by Weinberg (1908; Figure 3) laid the foundation for the field of population genetics (Crow 1999; Edwards 2008).
The Hardy-Weinberg Equilibrium

The Hardy-Weinberg Theorem deals with Mendelian genetics in the context of populations of diploid, sexually reproducing individuals. Given a set of assumptions (discussed below), this theorem states that:

1. allele frequencies in a population will not change from generation to generation.
2. if the allele frequencies in a population with two alleles at a locus are \( p \) and \( q \), then the expected genotype frequencies are \( p^2 \), \( 2pq \), and \( q^2 \). This frequency distribution will not change from generation to generation once a population is in Hardy-Weinberg equilibrium. For example, if the frequency of allele \( A \) in the population is \( p \) and the frequency of allele \( a \) in the population is \( q \), then the frequency of genotype \( AA = p^2 \), the frequency of genotype \( Aa = 2pq \), and the frequency of genotype \( aa = q^2 \). If there are only two alleles at a locus, then \( p + q \) by mathematical necessity, equals one. The Hardy-Weinberg genotype frequencies, \( p^2 + 2pq + q^2 \), represent the binomial expansion of \( (p + q)^2 \), and also sum to one (as must the frequencies of all genotypes in any population, whether it is in Hardy-Weinberg equilibrium). It is possible to apply the Hardy-Weinberg Theorem to loci with more than two alleles, in which case the expected genotype frequencies are given by the multinomial expansion for all \( k \) alleles segregating in the population: \( p_1^1p_2^1\ldots = \ldots pk^k \).

The conclusions of the Hardy-Weinberg Theorem apply only when the population conforms to the following assumptions:

1. **Natural selection** is not acting on the locus in question (i.e., there are no consistent differences in probabilities of survival or reproduction among genotypes).
2. Neither mutation (the origin of new alleles) nor migration (the movement of individuals and their genes into or out of the population) is introducing new alleles into the population.
3. Population size is infinite, which means that genetic drift is not causing random changes in allele frequencies due to sampling error from one generation to the next. Of course, all natural populations are finite and thus subject to drift, but we expect the effects of drift to be more pronounced in small than in large populations.
4. Individuals in the population mate randomly with respect to the locus in question. Although nonrandom mating does not change allele frequencies from one generation to the next if the other assumptions hold, it can generate deviations from expected genotype frequencies, and it can set the stage for natural selection to cause evolutionary change.

If the genotype frequencies in a population deviate from Hardy-Weinberg expectations, it takes only one generation of random mating to bring them into the equilibrium proportions, provided that the above assumptions hold, that allele frequencies are equal in males and females (or else that individuals are hermaphrodites), and that the locus is autosomal. If allele frequencies differ between the sexes, it takes two generations of random mating to attain Hardy-Weinberg equilibrium. Sex-linked loci require multiple generations to attain equilibrium because one sex has two copies of the gene and the other sex has only one.

Given these conditions, it is easy to derive the expected Hardy-Weinberg genotype frequencies if we think about random mating in terms of the probability of producing each genotype via random union of gametes into zygotes (Table 1). If each allele occurs at the same frequencies in sperm and eggs, and gametes unite at random to produce zygotes, then the probability that any two alleles will combine to form a particular genotype equals the product of the allele frequencies. Since there are two ways of generating the heterozygous genotype (\( Aa \) egg and a sperm, or a egg and \( A \) sperm), we sum the probabilities of those two types of union to arrive at the expected Hardy-Weinberg frequency of the heterozygous genotype (2pq).

```
<table>
<thead>
<tr>
<th>eggs</th>
<th>sperm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>a (g)</td>
<td>A (p)</td>
</tr>
<tr>
<td>a (g)</td>
<td>A (p)</td>
</tr>
</tbody>
</table>

Table 1: A Punnett square depicting the probabilities of generating all possible genotypes at a diallelic Mendelian locus in a population that conforms to Hardy-Weinberg assumptions.
```

It is important to recognize that the Hardy-Weinberg equilibrium is a neutral equilibrium, which means that a population perturbed from its Hardy-Weinberg genotype frequencies will indeed reach equilibrium after a single generation of random mating (if it conforms to the other assumptions of the theorem), but it will be a new equilibrium if allele frequencies have changed. This property distinguishes a neutral equilibrium from a stable equilibrium, in which a perturbed system returns to the same equilibrium state. It makes sense that the Hardy-Weinberg equilibrium is not stable, since a change from the equilibrium genotype frequencies will generally be associated with a change in allele frequencies (\( p \) and \( q \)), which will in turn lead to new values of \( p^2 \), \( 2pq \), and \( q^2 \). Thereafter, a population that meets Hardy-Weinberg assumptions will remain at the new equilibrium until perturbed again.

Given a population in which we know the number of individuals with each genotype, we can test for statistical deviation from Hardy-Weinberg equilibrium using a simple chi-square goodness-of-fit test or a more powerful exact test. The latter class of methods has proved particularly useful for large-scale genomic studies, in which scientists evaluate thousands of loci segregating for multiple alleles (Wiggington et al. 2006). Observed genotype proportions in natural populations typically conform to Hardy-Weinberg expectations, as we might expect given that a population perturbed from equilibrium can achieve new equilibrium frequencies after only one generation of random mating.

Although statistical deviation from Hardy-Weinberg expectations generally indicates violation of the assumptions of the theorem, the converse is not necessarily true. Some forms of natural selection (e.g., balancing selection, which maintains multiple alleles in a population) can generate genotypic frequency distributions that conform to Hardy-Weinberg expectations. It may also be true that migration or mutation is occurring, but at such low rates as...
Evolutionary Implications of the Hardy-Weinberg Theorem

The Hardy-Weinberg Theorem demonstrates that Mendelian loci segregating for multiple alleles in diploid populations will retain predictable levels of genetic variation in the absence of forces that change allele frequencies. A common way of visualizing these expectations is to plot $p^2$, $2pq$ and $q^2$ as a function of allele frequencies (Figure 4). This graphical presentation emphasizes two important consequences of the Hardy-Weinberg principle:

1. Population heterozygosity (the frequency of heterozygotes) is highest when $p = q = 0.5$.
2. Rare alleles are found primarily in heterozygotes, as they must be, given that $q^2$ is much smaller than $2pq$ when $q$ is near zero, and $p^2$ is much smaller than $2pq$ when $p$ is near zero.

The second point takes on particular significance if we consider the potential for natural selection to influence the frequencies of new mutations. If a population conforms to all other Hardy-Weinberg assumptions, selection will eventually fix an advantageous allele in the population such that all individuals are homozygous for that allele. The initial increase in frequency of a rare, advantageous, dominant allele is more rapid than that of a rare, advantageous, recessive allele. This is because, as we have seen, rare alleles are found mostly in heterozygotes, such that a new recessive mutation can’t be “seen” by natural selection until it reaches a high enough frequency (perhaps by drift in a real, finite population) to start appearing in homozygotes. A new dominant mutation, however, is immediately visible to natural selection because its effect on fitness is seen in heterozygotes. Thus, although Hardy (1908) demonstrated that dominance alone does not change allele frequencies at a locus, the dominance relationships among alleles can have substantial influence on evolutionary trajectories.

![Figure 4: A plot of Hardy-Weinberg equilibrium genotype frequencies (p to the 2, 2pq, q to the 2) as a function of allele frequencies (p and q).](image)

Selection, mutation, migration, and genetic drift are the mechanisms that effect changes in allele frequencies, and when one or more of these forces are acting, the population violates Hardy-Weinberg assumptions, and evolution occurs. The Hardy-Weinberg Theorem thus constitutes a null model for the discipline of population genetics, and is fundamental to the study of evolution.

References and Recommended Reading

Using Molecular Techniques to Answer Ecological Questions

By: Kirsten J. Monsen-Collar (Biology and Molecular Biology Department, Montclair State University) & Paola Dolcemascolo (Earth and Environmental Studies Department, Montclair State University) © 2010 Nature Education

This article explores the tools used in molecular ecology and how these tools enhance traditional ecological studies. Also, it examines a number of seminal studies that have used molecular ecology tools and discusses the limitations of molecular ecology.

The Beginnings of Molecular Ecology

As far back as the late 1800s, researchers realized that answers to some ecological questions could be obtained by examining the molecular composition of organisms. One of the earliest attempts at using molecules to address an ecological question was by Church in the late 1860s. Church studied relationships among birds and found that the pigment turacin was present only in birds of the Musophagidae family (Figure 1). He and others went on to determine that evolutionary relationships could be inferred according to whether species shared particular molecules. Early studies were limited to organic molecules obtained through diet and so may at times have confused relationships among organisms. However, the idea that the study of molecules could be a useful technique for understanding animals, their relationships, and their evolution had been firmly planted within the mind of the scientific community. And it is from this idea that the discipline of molecular ecology eventually emerged.

![Figure 1: Musophaga rossae, one of the bird species with turacin in its feathers](https://www.nature.com/scitable/knowledge/library/using-molecular-techniques-to-answer-e...)

What exactly is molecular ecology? As we will see, it is an interdisciplinary approach to some of the most fundamental questions in organismal biology. Some scientists today do not consider it to be its own discipline but rather an "approach" taken in certain cases to answer certain questions. Most scientists, however, agree that it is distinct from other studies of organismal biology. Molecular ecology is defined as "the application of molecular..."
Molecular techniques to answer ecological questions” (Beebee & Rowe 2004). In this article we explore the tools used in molecular ecology and how these tools enhance traditional ecological studies. We examine a number of seminal studies that have used molecular ecology tools. We also discuss the limitations of molecular ecology.

**Tools of the Trade**

Molecular ecology’s development as a field of study can be seen to run parallel to advances in what would become the tool of the trade: the molecular marker. Molecular markers are sections of an organismal genome. These sections of DNA can be more readily obtained through a procedure known as the polymerase chain reaction (PCR) (Figure 2). There are many different types of DNA markers used in molecular ecology, including: microsatellites (highly repetitive sequences of DNA that mutate rapidly and are often used to identify individuals), minisatellites (similar to microsatellites but with longer repetitive sequences), restriction fragment length polymorphisms (RFLPs, specific sites of DNA that can be cut by enzymes yielding different-sized fragments of DNA in different species, populations, and — rarely — individuals), and DNA sequence data (the bases of DNA are determined and similarities and differences are compared to identify species, populations, and individuals) (Figure 3). These markers are by no means a comprehensive list, and the marker (or markers) one chooses to use depends greatly on the type of question being addressed in the study.

One of the reasons why molecular ecology has advanced rapidly as a field of study is the advent of PCR. PCR makes it possible to amplify billions of copies of a specific piece of DNA from the genome with very few starting copies. In other words, it is possible to take a small sample of tissue to obtain enough DNA for study. This contrasts with earlier approaches that often required large amounts of DNA or protein, which often meant killing the organism of study. Obviously, killing one’s study organism can be counterproductive, particularly if the intent of the study is to advance conservation efforts or protect endangered species. The fact that only a small starting amount of DNA is needed now for molecular ecology studies has opened the door for non-invasive sampling methods. It is now possible to isolate DNA from hair, urine, shed skin, and feces, thus preventing harm to endangered and non-endangered species. PCR also amplifies old and/or degraded DNA, such as that found in fossils (Figure 2).

The development of molecular markers has led to an explosion of studies that have used them to answer questions ranging from relatedness among species, to the evolutionary history of populations, the amount of genetic variation within a species, patterns of behavior, how patterns of gene expression can vary among closely related populations, and many other aspects of organismal variation. For example, in one of the earliest molecular ecological studies, O’Brien and his colleagues (1983) found that the genetic diversity among cheetahs in South Africa was extremely low (Figure 4). In fact, O’Brien et al. (1985) transplanted skin grafts between different cheetahs and found that the cheetahs were so genetically similar, their immune systems did not reject the tissue grafts. This and other early studies triggered the debate, which continues today, over the importance of genetic diversity to the persistence of a population and how genetic diversity is related to environmental change. If every organism in a population has the same genetic make up, it is likely each will respond the same way to any environmental change. If this environmental change hinders an organism’s ability to survive or reproduce, it is probable that all genetically similar individuals in the population will be affected in the same way, thus increasing the chance of extinction. However, this is not always the case since some genetically similar populations appear to thrive. As such, the importance of genetic diversity for population survival continues to be a subject of debate.

**Moving Beyond Traditional Ecological Approaches**

Molecular techniques can be useful to, and sometimes necessary for, the field of ecology. Traditional approaches to ecology have limitations that can sometimes be addressed with molecular techniques. For one, traditional ecological approaches have relatively narrow timeframes of observation. Unless a long history of data has been directly collected on a particular organism through the years, traditional ecological approaches are limited to the period over which a study is conducted. Extrapolations can be made, but support for these extrapolations can be tenuous. On the other hand, historical events leave distinct signatures in the molecules of organisms that can be accurately interpreted.
The divergence time between species, for example, can be readily calculated provided the divergence can be associated with significant historical and environmental events. For instance, if one can associate the divergence between two species with a known geologic event, one can calibrate a molecular clock. In turn, a molecular clock can be used to determine the time since other species diverged from each other based on the amount of genetic differences observed at a specific molecular marker. 

Beerli et al. (1996) were able to calibrate a protein clock for populations of the Rana esculenta frog group separated by saltwater barriers in the Aegean Sea using known geologic dates of island isolation. Since frogs can't survive in salt water, they were most likely separated when these salt water barriers appeared. As a result, the researchers were able to date the separation of frogs on these islands. They then measured how many genetic differences exist between these groups and used these data to estimate how many genetic changes occurred over time.

A second important limitation of traditional ecological approaches is dependence on direct observation. One of the most commonly used methods of tracking animal movements and immigration into new populations is telemetry (Figure 5). Simply understanding an animal's physical movement from one place to another, however, often gives an incomplete picture of that animal's behavior and how it relates to its environment. One fundamental limitation of telemetry is that it cannot detect whether a dispersing animal successfully mates in its new territory or upon joining a new population. Reproductive success is an indication of fitness and, therefore, of the long-term survival of a population — a fundamental issue in ecology. But a DNA-based approach can provide much more insight into the mating behaviors of dispersing animals. By looking at molecular markers in a particular group of animals, researchers can establish the familial relationships among the members of that group; therefore, they can get an accurate picture of who is mating with whom. Recent immigrants will have slight differences in their molecular markers and they can be identified. If those immigrants are mating successfully in their new group, those differences will be passed onto their offspring and will appear more frequently. If immigrants do not mate, those differences will disappear.

Finally, since traditional ecological approaches are based on direct observations of organisms, they frequently do not detect underlying variation in organisms that does not influence physical appearances. It is possible for organisms to appear the same physically while exhibiting as much genetic divergence as found between distinct species. Cryptic variation can sometimes only be detected by comparing DNA.

These examples are intended to illustrate how molecular techniques can supplement and enhance information gained through traditional methodologies. We can get an even better idea of how molecular techniques have refined traditional ecology by looking at some of the fundamental questions answered by molecular ecology.

**Answering Ecological Questions with Molecular Techniques**

Some of the earliest molecular ecology studies involved examining the mating systems of birds. It was long thought that birds were monogamous. DNA samples of parents and their offspring challenged this idea. Indeed, it was found that extra-pair copulations were very frequent among bird species thought to be monogamous. As a result of the extensive use of DNA sampling of parents and their offspring, it is now understood that only a very small number of bird species adhere to a strictly monogamous mating system. Mating behaviors have also been described using molecular techniques in many other organisms including (among others) pipefish, frogs, beetles, and turtles.

Our understanding of habitat use has changed as the result of molecular techniques. Habitat use can be relatively simple to assess when animals can be tracked and directly observed using their habitat. But what happens when specific patterns of habitat use cannot be directly observed? There have been a number of studies on genetic structuring of populations that appeared to be uniformly distributed across a particular landscape. These studies found that populations were highly structured, indicating that organisms preferred to settle and mate in certain habitats over others. These findings contradicted observed distribution patterns at the landscape level because observational approaches were unable to track mating patterns.

Early studies involving use of molecular techniques also found evidence of extreme variation among apparently physically-identical individuals within a species. Indeed, several studies among salamanders of the genus Plethodon demonstrated extreme genetic divergence among animals that appeared identical. These early studies also demonstrated a mixture of different Plethodontid genomes within individuals, providing evidence of hybridization between different species, information that was not yet available by traditional ecological methods. Identifying cryptic species has become extremely important in the field of conservation genetics, especially with regard to the protection of endangered species. For example, the spotted frog *Rana pretiosa*, which occurs in the Pacific Northwest of the United States, displays almost no physical variation among populations (Figure 6). However, genetic analysis has revealed that populations in Oregon are as genetically distinct from other populations in the Pacific Northwest as separate species. The discovery of genetic divergence within the species led to the classification of two separate species, both of which are now protected. The existence of cryptic species is not surprising given that these organisms, and many others, often rely on non-visual cues, such as chemicals and/or sound, to identify a mate. Molecular ecology has allowed researchers to explore why there are genetic differences in the absence of morphological differences. Not only does molecular ecology allow the detection of genetic differences, but it also allows for the interpretation of how the differences came to be since certain phenomena (e.g., natural selection, mate choice, differential habitat use) may leave different genetic signatures.

Molecular approaches have also played a significant role in endangered species conservation besides addressing the question of cryptic variation. For example, molecular studies have been used to identify migration corridors between populations that can prevent isolation of endangered populations. Molecular approaches have also been used to identify ideal populations for transfer to extinct or declining populations, methods for maximizing genetic variation in captive-bred animals, and species identification of contraband goods. Identifying species has been especially important for prosecuting poachers for harvesting endangered species when the only remains of the harvested animal is a piece of meat, bone, or fur. In fact, molecular techniques have been developed that can identify species based on the DNA from tissue even if the tissue has been cooked and mixed with other ingredients.

**Limitations of Molecular Ecology**

Molecular ecology has important limitations to consider. First, marker development can be time-consuming and expensive. Second, while it can be beneficial that molecular ecology is not dependent on direct observation of behaviors, this benefit can often be a limitation. Since the behavior is not directly observed, scientists must deduce the behavior that led to a specific molecular pattern, and there can often be multiple explanations for the same observed pattern. Third, it is not practical to look at the entire genome of all organisms, so one must look at a small subset of markers. Different markers may show discordant patterns or may not be representative of the entire genome. Finally, there are some questions that molecular ecology simply cannot answer and must be addressed with direct observation. For example, some behaviors important to the natural history of an organism, such as parental care and courtship behavior, can only be documented through direct observation.
References and Recommended Reading


Mutations Are the Raw Materials of Evolution

By: Joel L. Carlin (Department of Biology, Gustavus Adolphus) © 2011 Nature Education


A mutation is a change in the sequence of an organism’s DNA. What causes a mutation? Mutations can be caused by high-energy sources such as radiation or by chemicals in the environment. They can also appear spontaneously during the replication of DNA.

Mutations generally fall into two types: point mutations and chromosomal aberrations. In point mutations, one base pair is changed. The human genome, for example, contains over 3.1 billion bases of DNA, and each base must be faithfully replicated for cell division to occur. Mistakes, although surprisingly rare, do happen. About one in every $10^{10}$ (10,000,000,000) base pair is changed. The most common type of mistake is a point substitution. More uncommon is the failure to copy one of the bases (deletion), the making of two copies for a single base (point duplication) or the addition of a new base or even several bases (insertion). Chromosomal aberrations are larger-scale mutations that can occur during meiosis in unequal crossing over events, slippage during DNA recombination or due to the activities of transposable events. Genes and even whole chromosomes can be substituted, duplicated, or deleted due to these errors (Figure 1).

![Figure 1: Mutations in DNA sequence from seven related species of tropical fishes (data are from intron 6 of LDH-A gene sequenced by the author from epinepheline serranids)](image)

Mutations can have a range of effects. They can often be harmful. Others have little or no detrimental effect. And sometimes, although very rarely, the change in DNA sequence may even turn out to be beneficial to the organism.

A mutation that occurs in body cells that are not passed along to subsequent generations is a somatic mutation. A mutation that occurs in a gamete or in a cell that gives rise to gametes is special because they impact the next generation and may not affect the adult at all. Such changes are called germ-line mutations because they occur in a cell used in reproduction (germ cell), giving the change a chance to become more numerous over time. If the mutation has a deleterious affect on the phenotype of the offspring, the mutation is referred to as a genetic disorder. Alternately, if the mutation has a positive affect on the fitness of the offspring, it is called an adaptation. Thus, all mutations that affect the fitness of future generations are agents of evolution.

Mutations are essential to evolution. Every genetic feature in every organism was, initially, the result of a mutation. The new genetic variant (allele) spreads via reproduction, and differential reproduction is a defining aspect of evolution. It is easy to understand how a mutation that allows an organism to feed, grow or reproduce more effectively could cause the mutant allele to become more abundant over time. Soon the population may be quite
Mutations Are the Raw Materials of Evolution

Some individuals having greater evolutionary fitness. Whether that fitness is affected by genetic disorders, venomous saliva or enlarged offspring, heritable variation can only arise by mutation. Evolution is simply not possible without random genetic change for its raw material.

Interbreeding individual plants with the largest fruits and seeds in the process of artificial selection, creating many of our modern agricultural crop. Mistake occurred in reproductive organs, was successfully passed on to future generations. Humans themselves have mimicked this process by compared to other grasses, and this is often due to the genomic duplications that occurred in the ancestors of modern rice and wheat and, because the flowering plant! Most cereals that humans eat have enormous seeds or fruits, a trait that can be of distinct advantage if you are a vertebrate. Flowering plants have a different mixture from other venomous snake families. The ancestors of sea snakes, coral snakes, and cobras (family Elapidae) evolved venom that attacks the nervous system while the venom of vipers (family Viperidae, including rattlesnakes and the bushmaster) acts upon the cardiovascular system. Both families have many different species that inherited a slight advantage in venom power from their ancestors, and as mutations accumulate the diversity of venoms and diversity of species increased over time.

Although the history of many species have been affected by the gradual accumulation of tiny point mutations, sometimes evolution works much more quickly. Several types of organisms have an ancestor that failed to undergo meiosis correctly prior to sexual reproduction, resulting in a total duplication of every chromosome pair. Such a process created an "instant speciation" event in the gray treefrog of North America (Figure 2).

The consequence of doubling the genome size in plants is often abnormally large seeds or fruits, a trait that can be of distinct advantage if you are a flowering plant! Most cereals that humans eat have enormous seeds compared to other grasses, and this is often due to the genomic duplications that occurred in the ancestors of modern rice and wheat and, because the mistake occurred in reproductive organs, was successfully passed on to future generations. Humans themselves have mimicked this process by interbreeding individual plants with the largest fruits and seeds in the process of artificial selection, creating many of our modern agricultural crop strains. The idea of evolution by natural selection, first described by Charles Darwin and Alfred Russell Wallace, requires differential survival due to some individuals having greater evolutionary fitness. Whether that fitness is affected by genetic disorders, venomous saliva or enlarged offspring, heritable variation can only arise by mutation. Evolution is simply not possible without random genetic change for its raw material.

References and Recommended Reading


Why Are Life Histories So Variable?

By Richard P. Shefferson (Odum School of Ecology, University of Georgia) © 2010 Nature Education


The life spans of plants, animals, and microbes range from minutes to millennia. Some reproduce only once and others many times. Why are life histories so diverse?

Imagine an organism capable of producing infinite numbers of offspring and living forever. This hypothetical organism is referred to as a Darwinian demon, and one has never evolved into being (Law 1979). Instead, evolution has resulted in a diversity of life histories including all combinations of reproduction, life span, and life stages. Why has this diversity evolved?

Life Histories as Evolutionary Responses

A life history is a unique combination of developmental stages and demographic events comprising what an organism goes through from birth to death. At their most basic, life histories may be modeled as series of major life stages, each with its own probabilities of mortality and transition, and rates of fertility (Figure 1). Among the first to consider the evolution of specific life history strategies was Lamont Cole. Cole suggested that, all else being equal, the advantage of living and reproducing more than one year was not much more than if an annual life history were maintained (Cole 1954). The fact that nature includes a diversity of long- and short-lived organisms reproducing once to many times contradicts Cole’s hypothesis and led it to be termed Cole’s paradox (Charnov & Schaffer 1973). Cole’s model is now seen as too simplistic because mortality, reproduction, and other aspects of life histories vary within populations due both to factors inherent in the organism, referred to as intrinsic factors, and to environmental factors, referred to as extrinsic factors. Life histories are evolved responses to these sets of factors.

Intrinsic factors include relationships among genes, as well as among physiological, behavioral, and demographic traits. Such relationships are commonly referred to as trade-offs or costs because of the commonness of negative relationships among traits, particularly under the physical limits imposed by finite stores of resources. Trade-offs imply that the evolution of a trait both involves impacts on other traits and is constrained by these relationships. For example, higher allocation of resources to growth as an adult may come at a cost to current reproduction, which may also require significant inputs of resources. However, this same allocation to growth may decrease adult mortality, increasing the chance that an adult will reproduce in the future.

Trade-offs are complicated by associations among the genes responsible for them, as well as by patterns in resource allocation (de Jong 1993). For example, two traits X and Y may occur in the same combinations more often than expected by chance due to past evolution or the same or nearby genes controlling their expression, resulting in linkage between the traits. Here, natural selection favoring a particular value for trait X will also inevitably cause Y to be positively but indirectly selected. Such patterns can also arise if individuals in a population vary systematically in their allocation patterns to each trait, causing correlations among life history trait values (Figure 2). Finally, some trade-offs can favor the evolution of complex life histories. For example, the trade-off between parental care of self v. care of offspring is thought to have favored the evolution of larval stages in many kinds of organisms, including amphibians and insects. Because the diet of a larva is typically different from that of an adult of the same species, the production of larvae reduces the possibility of food competition between parent and offspring.

Environmental Variation

Life histories evolve in response to the environment (i.e., extrinsic factors) as well as to internal constraints. The environment is continually changing, giving natural selection a “moving target”. The Red Queen hypothesis states that the tendency for natural selection to change over time, due to continual change in the environment, creates a situation in which no organism is perfectly adapted and all species continually evolve (van Valen 1973). The hypothesis’ name is a reference to the character in Lewis Carroll’s book, Through the Looking-Glass, who tells Alice that it takes all her energy to run just to stay in the same place.

The degree and pattern of environmental variation can favor specific life history strategies. Environmental variability can be temporal or spatial and deterministic, stochastic, or predictable. Deterministic environmental variability is a shift in an environmental factor away from the previous mean and is not thought to commonly result in the evolution of specific life histories. For example, current climate change is a deterministic change toward a warmer climate, and its main impact on species is likely to be to cause changes in geographic distribution. Stochastic environmental variability is random variation in an environmental factor and does not involve long-term changes in the mean value of the factor.

Predictable environmental variability is
Random Variation

Stochastic environmental variability favors changes in life span and reproductive strategy. This kind of variability most often causes evolutionary response via natural selection on juveniles. Juveniles have a stronger relationship to fitness than mature individuals, due to the generally negative relationship between age and fitness impact (Hamilton 1966). Increased mortality and variability in mortality in the juvenile period both favor the evolution of delayed reproduction, provided that delaying reproduction increases the chance of producing viable offspring. The chance of producing viable offspring may increase if the individual gains a greater ability to produce greater numbers of offspring or to produce offspring of greater quality (Figure 3). Such an increase in juvenile mortality may also favor a longer reproductive life span. In contrast, decreased juvenile mortality favors the evolution of earlier maturity. When extreme, stochastic environmental variation can involve catastrophes. Although catastrophes may wipe populations out of existence, they also introduce strong selection for life stages capable of tolerating harsh environmental conditions.

Stochastic environmental variation may favor the evolution of bet-hedging traits. These traits involve an apparent drop in fitness in the short-term in order to maximize fitness in the long-term. Fitness is a geometric property, meaning that it is multiplicative rather than additive across generations. Its geometric nature means that mean fitness is more strongly influenced by harsh periods than favorable periods, and so increased variability in fitness causes mean fitness to drop across generations. Bet-hedging traits counteract the influence of harsh periods on fitness by stabilizing the variation in fitness over time. By stabilizing fitness over the long-term, bet-hedging traits may be favored over other traits that appear to convey greater fitness in the short-term. Vegetative dormancy in herbaceous plants may be one such trait because although it involves the foregoing of reproduction and sprouting in a particular year, it may also prevent mortality from increasing to substantial levels and make future reproduction more likely (Shefferson 2009; Figure 4).

Predictable Environmental Variation

Predictable environmental variation involves temporal cycles between different environmental conditions. Such cycles are routine and repeated, and do not change dramatically in any random or deterministic ways. This kind of variation favors the evolution of timed and often cyclical life history strategies. Examples include seasonal or diurnal resting stages, such as hibernation in mammals, winter-dormant seeds, and programmed senescence in annual plants (Roach 1993). The overall impact of predictable variation on life histories is the evolution of additional life stages and potentially complex life cycles.

Cyclical variation in the environment causes natural selection to favor different strategies at different times. **Phenotypic plasticity**, in which one genotype produces different phenotypes under different environmental conditions, is a common result (Schlichting 1986). Phenotypic plasticity can include gradual change in a trait or dramatic and discrete change from time to time. As an example of dramatic change, plants often flower according to a mechanism of discrete phenotypic plasticity, in which they sense seasonal changes in red/far-red light ratios, and use them to sprout at the proper time of the year. As an example of gradual change, within a growing season, plant growth will change to compensate for expected patterns in precipitation and temperature, as well as available nutrients.

Historical Contingency

Evolutionary history can impact the evolution of life history strategies by making some strategies more or less likely to evolve. Life histories exhibit some degree of phylogenetic signal, meaning that closely related species share similar evolutionary responses due to stronger biological similarities than among more distantly related species. Phylogenetic signal is typically due to the evolution of specific traits and genetic systems controlling them, including those that are phenotypically plastic, which are then passed down to all species derived from that particular ancestor species (Figure 5). Some such traits become fixed in a group of related species, while others still evolve, though not necessarily at the same rate among all such groups. These evolutionary events create constraints on evolution, such that extreme deviations from what previously evolved are unlikely.

References and Recommended Reading


Explore This Topic

BASIC

- Evolution Is Change in the Inherited Traits of a Population through Successive Generations
- The Hardy-Weinberg Principle
- Using Molecular Techniques to Answer Ecological Questions
- Mutations Are the Raw Materials of Evolution

ADVANCED

- Avian Egg Coloration and Visual Ecology
- The Ecology of Avian Brood Parasitism
- The Geography and Ecology of Diversification in Neotropical Freshwaters
- The Maintenance of Species Diversity
- Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations
- Neutral Theory of Species Diversity
- Population Genomics
- Semelparity and Iteroparity

INTERMEDIATE

- Why Are Life Histories So Variable?
- Comparative Genomics
- Case Study: The Glorious, Golden, and Gigantic Quaking Aspen
- Cybertaxonomy and Ecology
- Molecular Genetic Techniques and Markers for Ecological Research
- Resource Partitioning and Why It Matters


Comparative Genomics

By: Jeffrey Touchman (School of Life Sciences, Arizona State University) © 2010 Nature Education


Comparison of whole genome sequences provides a highly detailed view of how organisms are related to each other at the genetic level. How are genomes compared and what can these findings tell us about how the overall structure of genes and genomes have evolved?

**What Is a Genome Made Of?**

Although living creatures look and behave in a myriad of ways, all of their genomes consist of DNA, the chemical chain that harbors the genes that code for thousands of different kinds of proteins. Within DNA are the instructions sufficient to make an organism and the means by which organisms pass information along to their offspring. Remarkably, this information is coded by only four nucleotides: adenine (A), cytosine (C), guanine (G), and thymine (T). Understanding the order of these nucleotides in linear DNA molecules has been an active pursuit since the discovery of DNA's double-helical structure (Watson et al. 1953). As such, DNA sequencing has emerged as a fundamental approach to molecular biology research. The power of DNA sequencing as a research tool has spurred the dramatic advancement of DNA sequencing technology, which is allowing ever more genomes to be sequenced and making comparative genomics an accessible focal point for the study of any form of life.

**What Genomes Have Been Sequenced?**

In addition to sequencing the three billion letters in the human “genetic instruction book” (Lander et al. 2001), researchers involved in the International Human Genome Project (HGP) sequenced the genomes of a number of important model organisms. These include chimpanzee (Lander et al. 2005), mouse (Waterston et al. 2002), rat (Gibbs et al. 2004), two puffer fish (Jaillon et al. 2004; Aparicio et al. 2002), fruit fly (Adams et al. 2000), two sea squirts (Dehal et al. 2002; Small et al. 2007), two roundworms (Stain et al. 2003; Stein et al. 1998), baker’s yeast (Goffeau et al. 1996), and the bacterium Escherichia coli (Blattner et al. 1997). Since the completion of the HGP, sequence drafts of the chicken (Blattnier et al. 2004), cow (Elsik et al. 2009), dog (Lindblad-Toh et al. 2005), honey bee (Lindblad-Toh et al. 2006), sea urchin (Sodergren et al. 2003; Stein et al. 2005), and the rosette squid Drosophila melanogaster (157 million base pairs v. 165 million base pairs, respectively) I possesses nearly twice as many genes (25,000 v. 13,000). In fact A. thaliana has approximately the same number of genes as humans (~25,000). Thus, a very early lesson learned in the “genomic era” is that genome size does not correlate with evolutionary status, nor is the number of genes proportionate to genome size.

**Comparative Genomics** is a field of biological research in which the genome sequences of different species — human, mouse, and a wide variety of other organisms from bacteria to chimpanzees — are compared. By comparing the sequences of genomes of different organisms, researchers can understand what, at the molecular level, distinguishes different life forms from each other. Comparative genomics also provides a powerful tool for studying evolutionary changes among organisms, helping to identify genes that are conserved or common among species, as well as genes that give each organism its unique characteristics.

**Intermediate (6)**

Ganjam
Goutham Kumar
lippman
Natesh
Ramanathan
Sathish Periyamasy
Thomas Elmermacher

**Advanced (8)**

Blogs
Creature Cast
MedSci Discoveries: Stay Fit & Stay Smart
Teach Ecology

**People Groups**

Ganjam
Goutham Kumar
lippman
Natesh
Ramanathan
Sathish Periyamasy
Thomas Elmermacher

**Recent Activity**

New post in Student Voices: Keeping Cool with Biomimicry
New topic in Women in Science: Kate Sleeth's First Guest Forum on Mentoring: Fish Needs Bicycle?
New post in MedSci Discoveries: Stay Fit & Stay Smart

**Related Topics**

Ecology
Evolution
Ecosystem Ecology
Physiological Ecology
Population Ecology
Community Ecology
Global and Regional Ecology
Conservation and Restoration
Animal Behavior
Teach Ecology

http://www.nature.com/scitable/knowledge/library/comparative-genomics-13239404
Finer-resolution comparisons are possible by direct DNA sequence comparisons between species. Figure 1 depicts a chromosome-level comparison of the human and mouse genomes that shows the level of synteny between these two mammals. Synteny is a situation in which genes are arranged in similar blocks in different species. The nature and extent of conservation of synteny differs substantially among chromosomes. For example, the X chromosomes are represented as single, reciprocal syntenic blocks. Human chromosome 20 corresponds entirely to a portion of mouse chromosome 2, with nearly perfect conservation of order along almost the entire length, disrupted only by a small central segment. Human chromosome 17 corresponds entirely to a portion of mouse chromosome 11. Other chromosomes, however, show evidence of more extensive interchromosomal rearrangement. Results such as these provide an extraordinary glimpse into the chromosomal changes that have shaped the mouse and human genomes since their divergence from a common ancestor 75–80 million years ago.

Comparison of discrete segments of genomes is also possible by aligning homologous DNA from different species. An example of such an alignment is shown in Figure 2, where a human gene (glycogen kinase: PKLR) and the corresponding PKLR homologs from macaque, dog, mouse, chicken, and zebrafish are aligned. Regions of high DNA sequence similarity with human across a 12-kilobase region of the PKLR gene are plotted for each organism. Notice the high degree of sequence similarity between human and macaque (two primates) in both PKLR exons (blue) as well as introns (red) and untranslated regions (light blue) of the gene. In contrast, the chicken and zebrafish alignments with human only show similarity to sequences in the coding exons; the rest of the sequence has diverged to a point where it can no longer be reliably aligned with the human DNA sequence. Using such computer-based analysis to zero in on the genomic features that have been preserved in multiple organisms over millions of years, researchers are able to locate the signals that represent the location of genes, as well as sequences that may regulate gene expression. Indeed, much of the functional parts of the human genome have been discovered or verified by this type of sequence comparison (Lander et al. 2001) and it is now a standard component of the analysis of every new genome sequence.

Table 1: Comparative genome sizes of humans and other model organisms

<table>
<thead>
<tr>
<th>Organism</th>
<th>Estimated size (base pairs)</th>
<th>Chromosome number</th>
<th>Estimated gene number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human (Homo sapiens)</td>
<td>3.0 billion</td>
<td>46</td>
<td>~25,000</td>
</tr>
<tr>
<td>Mouse (Mus musculus)</td>
<td>2.9 billion</td>
<td>40</td>
<td>~25,000</td>
</tr>
<tr>
<td>Fruit fly (Drosophila melanogaster)</td>
<td>165 million</td>
<td>8</td>
<td>~15,000</td>
</tr>
<tr>
<td>Plant (Arabidopsis thaliana)</td>
<td>157 million</td>
<td>10</td>
<td>~25,000</td>
</tr>
<tr>
<td>Roundworm (Caenorhabditis elegans)</td>
<td>91 million</td>
<td>12</td>
<td>~19,000</td>
</tr>
<tr>
<td>Yeast (Saccharomyces cerevisiae)</td>
<td>12 million</td>
<td>32</td>
<td>~6,000</td>
</tr>
<tr>
<td>Bacteria (Escherichia coli)</td>
<td>4.6 million</td>
<td>1</td>
<td>~3,200</td>
</tr>
</tbody>
</table>

Figure 1: Conserved segments in the human and mouse genome

Human chromosomes, with segments containing at least two genes whose order is conserved in the mouse genome as color blocks. Each color corresponds to a particular mouse chromosome. Centromeres, subcentromeric heterochromatin of chromosomes 1, 9 and 16, and the repetitive short arms of 13, 14, 15, 21 and 22 are in black. (International Human Genome Sequencing Consortium; Lander, E. S. et al. 2001)

Figure 2: Human PKLR gene region compared to the macaque, dog, mouse, chicken, and zebrafish genomes

Numbers on the vertical axis represent the proportion of identical nucleotides in a 100-bp window for a point on the plot. Numbers on the horizontal axis indicate the nucleotide position from the beginning of the 12-kilobase human genomic sequence. Peaks shaded in blue correspond to the PKLR coding regions. Peaks shaded in light blue correspond to PKLR mRNA untranslated regions. Peaks shaded in red correspond to conserved non-coding regions (CNSs), defined as areas where the average identity is > 70%. Alignment was generated using the sequence comparison tool VISTA (http://pipeline.lbl.gov).
We have learned from homologous sequence alignment that the information that can be gained by comparing two genomes together is largely dependent upon the phylogenetic distance between them. Phylogenetic distance is a measure of the degree of separation between two organisms or their genomes on an evolutionary scale, usually expressed as the number of accumulated sequence changes, number of years, or number of generations. The distances are often placed on phylogenetic trees, which show the deduced relationships among the organisms (Figure 3). The more distantly related two organisms are, the less sequence similarity or shared genomic features will be detected between them. Thus, only general insights about classes of shared genes can be gathered by genomic comparisons at very long phylogenetic distances (e.g., over one billion years since their separation). Over such very large distances, the order of genes and the signatures of sequences that regulate their transcription are rarely conserved.

At closer phylogenetic distances (50–200 million years of divergence), both functional and non-functional DNA is found within the conserved segments. In these cases, the functional sequences will show signatures of selection by virtue of their sequences having changed less, or more slowly than, non-functional DNA. Moreover, beyond the ability to discriminate functional from non-functional DNA, comparative genomics is also contributing to the identification of general classes of important DNA elements, such as coding exons of genes, non-coding RNAs, and some gene regulatory sites.

In contrast, very similar genomes separated by about 5 million years of evolution (such as human and chimpanzee) are particularly useful for finding the sequence differences that may account for subtle differences in biological form. These are sequence changes under directional selection, a process whereby natural selection favors a single phenotype and continuously shifts the allele frequency in one direction. Comparative genomics is thus a powerful and promising approach to biological discovery that becomes more and more informative as genomic sequence data accumulate.

What Are the Benefits of Comparative Genomics?

Dramatic results have emerged from the rapidly developing field of comparative genomics. Comparison of the fruit fly genome with the human genome reveals that about sixty percent of genes are conserved (Adams et al. 2000). That is, the two organisms appear to share a core set of genes. Researchers have also found that two-thirds of human genes known to be involved in cancer have counterparts in the fruit fly.

In addition to its implications for human health, comparative genomics may benefit the broader animal world and ecological studies as well. As sequencing technology grows easier and less expensive, it will find wide applications in agriculture, biotechnology, and zoology as a tool to tease apart the often-subtle differences among animal and plant species. Such efforts might also lead to the rearrangement of our understanding of some branches of the evolutionary “tree of life,” as well as point to new strategies for conserving rare and endangered species.

References and Recommended Reading


Case Study: The Glorious, Golden, and Gigantic Quaking Aspen

By: Michael Grant (Department of Ecology and Evolutionary Biology, University of Colorado at Boulder) & Jeffry Mitton (Department of Ecology and Evolutionary Biology, University of Colorado at Boulder) © 2010 Nature Education

Most massive living organism? Huge geographic range? Great beauty? A Phoenix species? What in the world?

Populus tremuloides, the quaking aspen of the North American continent, stands as one of the most easily recognized, most beautiful and most admired of all tree species. In order to help appreciate this magnificent species, we here highlight some of its key biological attributes.

Perhaps most impressively, along with its very similar sister species of European and Asian distribution — the Eurasian aspen (Populus tremula) — these two species occupy the broadest range of any tree species in the world. Why is that so?

Quaking aspen can be found from Alaska to Mexico and from Vancouver to Maine (Jones et al. 1985; Mitton & Grant 1996). In the north-central part of the continent, quaking aspen occurs at almost any elevation, while in the southern part of the US and in Mexico, it tends to be found only at higher elevations. A similar distribution pattern exists for Populus tremula in Europe and Asia. Admirers frequently note the striking white bark of quaking aspen. This bark lives and carries out photosynthesis, attributes that make it unique among North American trees and likely contribute to its impressive geographic range (Figure 1).

Figure 1: Living bark
The white bark is living tissue, unique among North American trees.

Aspen drops its leaves in winter but, of course, remains alive and thus requires metabolic energy. The soft tan to greenish hues often visible in aspen bark mark an important photosynthetic capability provided by the differing levels of chloroplasts. Stem photosynthesis contributes significantly to aspen’s...
over-wintering survival capabilities (Bervieller et al. 2007; Foote et al. 1978; Knowlton et al. 1976). The disadvantages of this type of bark include low fire resistance, ease with which people carve their initials in it and attractiveness as a food source for elk, numerous insects and fungi.

Aspen form individual patches comprised of numerous stems, termed ramets, each with its own trunk, branches, leaves and a shared root system (Figure 2). All of these structures arose from a single aspen seed, often in the very distant past; while these patches remain connected via root systems, they comprise a single clone. If the root system between patches is severed, the patches form physiologically separate entities but are generally still considered part of the same clone given that they are composed of genetically identical patches and parts, having been produced vegetatively. The boundaries of different clones stand out most clearly in the early spring when flowering and leafing-out occur (in that order). Aspen occur as males and females separately (dioecious), unlike the majority of tree species, which support both male and female reproductive parts on each individual (monoecious or hermaphroditic).

In early spring, an aspen clone will produce small, inconspicuous strings of reproductive parts called catkins, which are either male and produce pollen or female and produce eggs. Huge numbers of viable, tiny seeds mature and float off from the female on a tangle of cotton-like seed hairs that catch air currents, sometimes traveling great distances. Immediately after shedding their pollen and seeds, the clones then produce leaves that usually appear at the same time in all stems of a given clone. This time of the spring is when the boundaries of aspen clones stand out most visibly and reliably.

However, most aspen watchers tend to focus on the brilliant colors of aspen in the late fall prior to dropping their leaves (Figure 3). The dramatic visual show in the Rocky Mountains attracts many “leaf peepers” who find the brilliant gold, yellow, rose and even red leaf colors especially striking set against the dark green of their evergreen neighbors. But these color patches do not mark clonal boundaries as reliably as does leafing in the early spring because the chemical processes that produce the colors tend to be very sensitive to local micro-climate conditions such as aspect (whether north or south facing), soil moisture, etc. (personal observations). A single clone may exhibit multiple colors simultaneously. In aspen, all the pigments that give rise to these glorious colors can be found in the leaf from spring all the way through fall (see here). As summer begins to end and overnight temperatures drop, the aspen begin to first break down the green chlorophyll molecules that dominate the spring through summer color. The other pigment molecules — there all summer — then become more and more visible. This process reveals the golds, yellows and reds allowing aspen to really show their stuff until their leaves drop (Vogel 1993).
For many years, most western forest ecologists thought aspen reproduction from seeds was so rare as to warrant a publication of a single found seedling (Ellison 1943). However, it turns out that successful establishment of aspen via seeds occurs more frequently than previously thought (Mock et al. 2008). The ability of aspen to produce whole stands of “trees” vegetatively provides yet another key element in explaining the species’ ability to occupy huge geographic ranges.

There are several benefits of asexual expansion — spreading via roots which then send up shoots. As is true of other species of vegetatively-spreading plants (DeByle 1964; de Kroon & van Groenendael 1997; Jónsdóttir & Watson, 1997), one part of a clone might be near an important water source and for “I spread”; Grant 1993) represents the astonishing capabilities of an individual re-grow from the root system many times. Especially spectacular ones like the 1988 fires in Yellowstone National Park (Romme et al. 1997). Careful observers of steep mountainous slopes along the Rocky Mountain Cordillera will regularly see avalanche and mudslide tracks populated by young, light-green aspen clones re-colonizing those spaces with shoot densities up to 30,000 per acre (Jones et al. 1985). Similar patterns often follow forest fires. Rarely will a fire burn hot enough to kill the entire root system from which these stems arise, so an individual clone may occupy a given space and be completely wiped out on the surface but re-grow from the root system many times.

Indeed, one remarkable clone in the Fishlake National Forest named Pando (Latin for “I spread”†; Grant 1993) represents the astonishing capabilities of an individual clone to spread itself over a huge area (Barnes 1966, 1975; Grant et al. 1992). Pando covers about 107 acres and contains about 47,000 individual ramets, each complete with stem, branches and leaves (Barnes 1975; Grant et al. 1992; DeWoody et al. 2008). To date, this clone remains the most massive living organism ever reported with an estimated weight of at least 6,800 tons, exceeding that of the famous giant sequoia, General Sherman (Figure 4).

Given its size, it may also be very old, perhaps 80,000 years, but good dating of the time the original, tiny seed germinated and established this clone lies beyond current scientific capabilities. Plausible estimates have been offered ranging from several thousand to a million years in age, although recent molecular work argues that these may be overestimates (Barnes 1975; Mock et al. 2008). Whatever its age, Pando certainly represents one of the most remarkable individuals among all living organisms.

In order to have this single genotype occupy this space for those huge spans of time, the external environment must have had just the right balance of disturbance and stability. If an aspen stand does not experience periodic disturbances such as fire or avalanche, more shade-tolerant conifers tend to establish and shade out the high-light-requiring aspen stems. If the disturbances are too frequent, then the clone could not establish and spread to this extent.

Clone structure varies with geography but also varies due to the strong influences of rainfall and relative humidity. The largest clones generally occur in semi-arid environments such as the mountains of the western and southwestern US. Clones tend to be smaller in areas where the climate supports seed germination and establishment somewhat more readily (e.g., the eastern parts of North America and the upper Midwest).

The last particular attribute of quaking aspen we here highlight as important in contributing to its ability to occupy huge ranges derives from the comparatively high level of genetic variability among clones (Cheliak & Dancik 1982; Kanaga et al. 2008; Madritch et al. 2009; Mock et al. 2008). These interclonal levels of variability provide the raw material for evolutionary change across generation times. The large number of seeds produced from genetically variable sources generates an enormous array of potentially successful genotypes for establishment in newly opened areas and probably takes place at higher rates than previously thought by forest ecologists. These insights derive from the application of modern molecular techniques to quaking aspen in the field.

With only a bit of whimsy, we have saved one of the most obvious attributes for last: Why do quaking aspen leaves quake and tremble? The leaves of this species quake, shake and tremble in the presence of even the slightest breeze due to the physical structure of the leaf stem (petiole) which traces a flat, oblong, elliptical pattern when viewed in cross section (i.e., perpendicular to the stem itself) so it has strength in one dimension (the long part of the ellipse) and minimal strength in the second dimension (the narrow part of the ellipse), so even a gentle wind causes shaking, quaking and trembling.

We understand this phenomenon very well mechanically, yet a deeper question can be posed: Why does the petiole develop this way? Plant physiologists have pointed out several consequences of the trembling leaf behavior to include minimizing the risk of too much sunlight on the photosynthetic apparatus (photoinhibition), reducing the risk of overheating in intense, high elevation sunlight and improving photosynthetic rates by keeping a fresh supply of carbon dioxide near the leaf surface where the plant takes up that compound. Taking a different approach, one of our students did a small scale independent study several years ago where she identified matched pairs of aspen leaves and stabilized one with tubing to reduce its ability to tremble, then measured the amount of leaf damage due to insects near the end of the summer, comparing the leaves which could tremble with ones that could not. She found the insect damage to the “fixed” leaves was, on average, about 27% higher in the stabilized members of the pairs.

This tree species seems to almost have it all: powerful, opportunistic, sexual reproduction, long-distance seed dispersal, effective vegetative spread, clonal reproduction, regeneration from roots, high levels of genetic variability, living bark and a potentially enormous life span.

We anticipate that this glorious, golden, and gigantic species will provide great pleasure for future admirers of its beauty as well as revealing a rich trove of scientific insights as we learn from its enormously successful colonization of a huge geographic range.

References and Recommended Reading


http://www.nature.com/scitable/knowledge/library/case-study-the-glorious-golden-and-giga...


Grant, Michael C. "The Trembling Giant." Discover Magazine (October 1993).


Vogel, Steven. When leaves save the tree. Natural History 102, 48-63 (1993).
Cybertaxonomy and Ecology

By: Quentin Wheeler (School of Life Sciences, Arizona State University) & Antonio G. Valdecasas (Museo Nacional de Ciencias Naturales, CSIC) © 2010 Nature Education


What is cybertaxonomy and how will it advance the field of ecology?

Introduction

A revolution in taxonomic practice is underway that will make taxonomy an even more reliable source of information for ecologists. How taxonomic information is created, tested, accessed, thought about, and used, is changing dramatically with the emergence of cybertaxonomy.

What is Cybertaxonomy?

Cybertaxonomy is a contraction of “cyber-enabled taxonomy.” It shares the traditional goals of taxonomy: to explore, discover, characterize, name, and classify species; to study their phylogenetic relationships; and to map their geographic distributions and ecological associations. Through cybertaxonomy and the adoption of digital technologies, taxonomy is able to produce results faster and better than ever before (Wheeler 2008, 2010).

Cybertaxonomy should not be confused with the practice of creating databases of taxonomic information. Databases are an integral part of the process, but cybertaxonomy refers to a wide range of hardware, software, instrumentation, communication tools, and work practices that collectively allow taxonomists to do their work more efficiently while maintaining the highest levels of excellence. Consequently, users will find taxonomic information more reliable, comprehensive, and easily accessible.

Cybertaxonomy, like traditional taxonomy, is integrative. That is, taxonomists pull together, synthesize, and analyze all available evidence that is informative at the taxonomic level(s) being studied. Typical data sources include morphological, molecular, fossil, and ontogenetic as well as ethological, physiological, biochemical, and other sources of data, as appropriate. Cybertaxonomy can be visualized as a GIS-like environment with multiple data layers: morphological, distributional, molecular, image, and sound recordings (to name just a few). In addition, there are layers with algorithms and applications to process data in regard to phylogenetic, temporal, spatial, or ecological relations. Users may activate any combination of “layers” to retrieve desired information in a multi-layered “mesh”. The possibilities are numerous and diverse: dichotomous or interactive diagnostic keys, checklists of species in particular areas plotted over seasonal occurrences, distribution maps (point data or predicted ranges based on climate and environment), three-dimensional visualizations of phenotypic variation, etc. Just as individual taxonomists have traditionally synthesized all available knowledge into periodically published monographs, international teams of experts collaborating in cyberspace will be able to assemble and maintain, with up-to-the-minute accuracy, all data and information pertaining to the species of a taxon. Even these taxon knowledge bases will be combinable by ecologists seeking to compare and contrast species that co-occur (or might co-occur, given future climate change, for example) in a particular ecosystem.

State of Cybertaxonomy

When fully implemented, cybertaxonomy will impact nearly every aspect of the creation and use of taxonomic information. Taxonomists require research resources on a scale unlike that of any other life science discipline: primary literature dating back to 1753, thousands of specimens from the full geographic ranges of scores of related species, type specimens to assure nomenclatural stability, and specimens and data from dozens of museums or herbaria in many countries. Cybertaxonomy holds the promise of unprecedented access to such resources, including digital image archives, open-access databases, remotely operable instrumentation, and electronic publishing tools.

Traditional printed sources of taxonomic information are almost always out of date, often by the time of release. Since publication, there may be any number of new species, name changes, distribution records, or natural history observations added, all of which are of great value to the ecologist. Cybertaxonomy will open access to full and current information drawn from a taxon knowledge base that is constantly updated by the taxonomic community.

Cybertaxonomy will increase the arsenal of species identification tools available to the field ecologist, including browser-based field guides, interactive diagnostic keys, automated identifications from photographs, direct access to a specialist, or the collecting of tissue samples for molecular identifications — the latter uniquely useful for associating very dissimilar life stages such as those observed between larval and adult insects.

Uses of Taxonomic Information in Ecology

http://www.nature.com/scitable/knowledge/library/cybertaxonomy-and-ecology-15787535
As taxonomists make more species known, it will become possible to improve and better test assumptions and models on species diversity, distributions, co-occurrences, and co-varying factors; detect climate change; track species losses or gains; deepen our understanding of interactions among species in ecosystems; improve strategies and priorities for conservation; and predict the expansion or contraction of ranges. Among the uses for taxonomic information in ecology are:

**Species identifications**
Cybertaxonomy will provide a wide range of tools to assist in the immediate and accurate identification of species, the training of field ecologists to identify target taxa, and video-mediated consultation.

**Checklists**
Cybertaxonomy will make checklists available for particular localities and ecosystems that are complete and up to the minute.

**Names**
Scientific names are the unique identifiers used to store and retrieve what we know in databases and publications. Cybertaxonomy will allow taxonomists to improve the reliability, stability, and informativeness of names and to retrieve all relevant data and citations recorded under older names.

**Phylogenetic Classification**
By viewing species within their phylogenetic context, ecologists can make predictions about their contributions to ecological functions. Closely related species frequently have similar food sources, reproductive strategies, physiologies, and behaviors.

**Geographic Distributions**
Cybertaxonomy is mobilizing the information content of the natural history collections of the world, whose estimated three billion specimens provide a wealth of information about the distributions of species, including irreplaceable historical records.

**Virtual Ecological Assemblages**
For taxonomic research, specimens are curated according to their phylogenetic relationships. With the tools of cybertaxonomy, the ecologist can virtually reassemble all the specimens, regardless of taxon, collected in any one place at the same time or over a sequence of times.

**Conservation-relevant Information**
Cybertaxonomy will facilitate access to information about the status, abundance, and rarity of species, the species-richness of particular localities, and other data relevant to conservation evaluation and reserve designs.

**Morphologically Structured Information**
As image archives grow, incorporating both digitized publications and images of specimens, it will be possible to harvest and analyze such visual information to understand phenotypic variation in relation to environmental conditions, population structure, morphoclines, and other factors.

**Online Access to Museum Specimens**
Telemicroscopy has been used by pathologists and histologists for decades and will soon be able to network global collections such that actual specimens in addition to stored images may be accessed, manipulated, compared, measured, and studied in real time.

**Conclusions**
Cybertaxonomy is not only changing the way that taxonomists work but also the ways in which ecologists can access and make use of taxonomic data, information, and knowledge. As new ways to harvest, structure, and analyze taxonomic and related natural history information emerge, ecologists will be able to understand complex ecosystems in greater detail, detect and monitor environmental change more precisely, and more effectively achieve goals for sustainable ecological services.

**References and Recommended Reading**
Molecular Genetic Techniques and Markers for Ecological Research

By: Gerard J. Allan (Environmental Genetics & Genomics Facility, Dept. of Biology, Northern Arizona University) & Tamara L. Max (Environmental Genetics & Genomics Facility, Dept. of Biology, Northern Arizona University) © 2010 Nature Education

The recent union of molecular genetic methods and ecology is a great advance in evolutionary biology research. Molecular ecologists employ an array of molecular tools to study the genetic biodiversity of Earth.

Introduction

Ecology is inextricably intertwined with the evolutionary history of organisms. Through the process of descent with modification, organisms are continually passing genetic information from one generation to the next, information that is then recorded in the DNA of their descendents. Molecular biology's ability to access this record to better understand the origins of species and the ecological bases of their existence has become a cornerstone of modern ecological research.

In this article we briefly review the molecular tools and methods available to modern ecologists seeking a deeper understanding of the genetic bases of species formation, diversification, and evolutionary adaptation as they interact with ever-changing, complex environments.

PCR: An Ecologist's Best Friend

Most molecular-based studies begin with the extraction of DNA from a particular organism, followed by the amplification (i.e., generation of many copies) of particular segments of DNA using the polymerase chain reaction (PCR) (Figure 1). The utility of PCR lies in the fact that only minute quantities of DNA are needed (e.g., nanogram amounts). This is particularly useful when researchers are unable to obtain large amounts of tissue (e.g., as in the case of rare plant or animal species) or when numerous samples are needed, as in the case of population genetic studies. For example, an ecologist might ask: How genetically diverse are populations comprising a single species across a broad environmental gradient? The answer begins by obtaining DNA from different individuals from multiple populations and subjecting it to a PCR-based survey of genetic diversity. Such a survey can lead to inferences about the historical processes that led to differences in the genetic makeup of populations spanning a broad range of geographic and environmental conditions. Alternatively, one might want to know about the evolutionary history and relationships among members of a group of species. Consider, for instance, Darwin's finches (Figure 2). Once again, PCR is used to amplify particular coding or non-coding regions of DNA from different species, with the ultimate goal of reconstructing the phylogenetic history of each species within the complex. Once determined, the phylogenetic tree resulting from this study can provide information on how diverse the species complex is and which species are most closely related to one another (Figure 3). In turn, this can provide insight into the ecological (e.g., niche space use) and behavioral factors (e.g., foraging) that have contributed to the diversity of a species complex.
Figure 1: Polymerase chain reaction (PCR)
The PCR method begins with total genomic DNA extracted from an organism. The DNA is combined with site-specific primers, Taq polymerase, and other reagents (e.g., MgCl2, buffer, dNTPs) and subjected to repeated cycles, each of which consists of a denaturation phase, annealing phase and extension phase. Denaturation separates double-stranded DNA, allowing primers to anneal to specific sites, followed by incorporation of deoxynucleotide triphosphates (dNTPs; A, C, G, T), thereby extending the target site in the 5′-3′ direction (on both separated strands).

The first cycle is completed when one round of denaturation, annealing and extension is finished, resulting in two new copies of the target site. Subsequent cycles (typically 30-35) repeat the 3-phase process, resulting in many million-fold copies of amplified DNA.

© 2010 Nature Education All rights reserved.

Markers and Methods
There are many different types of DNA markers used in molecular ecology, including: microsatellites (MSATs, highly repetitive sequences of DNA that mutate rapidly and are often used to identify individuals), minisatellites (similar to microsatellites but with longer repetitive sequences), restriction fragment length polymorphisms (RFLPs, specific sites of DNA that can be cut by enzymes yielding different-sized fragments of DNA in different species, populations, and — rarely — individuals), and DNA sequence data (the bases of DNA are determined and similarities and differences are compared to identify species, populations, and individuals). Markers generated by these methods are also visualized in different ways. Traditionally, MSATs and RFLPs were visualized as discrete bands revealed by agarose gel electrophoresis. The nucleotides comprising DNA sequences, however, require finer levels of resolution, often achieved using polyacrylamide gels and autoradiography. Today, these marker types are typically visualized using chemiluminescence and genetic analyzers, which detect the fluorescent emission of labeled primers (as in the case of MSATs) or the fluorescently-labeled nucleotides of DNA sequences. These markers and visualization methods are by no means a comprehensive list, and the technique one chooses depends greatly on the type of question being addressed in the study. By understanding the different kinds of information provided by different marker methods, one can come to an informed decision on which is best for a particular study. Below, we describe three molecular methods commonly used in molecular ecological studies.

Figure 2: Darwin’s finches
There are three different classes of markers that can be easily distinguished based on the type of information they provide. Anonymous markers include those generated by a method called amplified fragment length polymorphisms (AFLPs) (Figure 4). This technique uses restriction enzymes combined with PCR to generate many thousands of unique fragments that can be used to genetically fingerprint individuals within or among species within the same genus. The utility of the AFLP method lies in that it does not require prior knowledge of an organism's genome. In other words, the regions of the genome that are targeted by this method are unknown to the investigator (hence, "anonymous"). Nevertheless, this method often provides a rich source of information about basic levels of genetic diversity and differentiation. AFLP markers are thus often used as a first step when investigating population or species differences. The downside to the use of AFLPs, however, is that they are somewhat limited in the type of information they can provide. For example, because these markers are of unknown origin and nucleotide composition (i.e., they simply constitute fragments of varying length within the genome), they are of limited use in reconstructing the evolutionary history of a group of organisms. Furthermore, AFLP markers are commonly referred to as dominant markers and are scored as being either "present" or "absent," which means that it is generally not possible to determine if a band on a gel represents a homozygous (AA) or heterozygous (Aa) genotype. This is because AFLP fragments represent unique restriction sites that are either present or absent in each individual and thus only one allele (if present) is amplified, thereby limiting the amount of information that can be obtained.

Another similar method called random amplified polymorphic DNA (RAPD) also generates dominant markers, which are typically viewed using agarose gel electrophoresis. This method, however, has largely been replaced by the AFLP method, which typically uses chemiluminescence and a genetic analyzer for visualization.

Another class of markers, known as sequence-tagged site (STS) markers, provides an alternative approach to characterizing genetic diversity within and among species. A sequence-tagged site is a short (200-500 bp) sequence of nucleotides that has a unique location within a genome and is targeted using PCR with primers designed by an investigator. One type of STS marker is represented by microsatellites (MSATs), also known as simple sequence repeats (SSRs) or variable number tandem repeats (VNTRs). Unlike AFLPs, these markers do require some knowledge of specific regions containing tandemly repeated nucleotide motifs, such as "ATC" or "GAG," which typically appear in non-coding regions of DNA. In combination with primers specifically designed to target these sites and amplification via PCR, the STS method provides a much finer level of discrimination among individuals. As codominant markers they are able to reveal whether an individual is heterozygous at a particular locus (e.g., Aa v. AA) because both alleles (A and a) are amplified during the PCR process. Given that their exact nucleotide composition (e.g., whether each repeat is always "ATC") is not always known, these markers share the same limitation as AFLPs for phylogenetic reconstruction because the homology of the markers is not known. One way to extend the utility of STS markers whose exact nucleotide composition is unknown is to sequence fragments derived from polymorphic loci. One marker method known as sequence characterized amplified regions (SCARs) uses fragments that have been cloned and sequenced to determine their exact nucleotide composition. Once sequenced, primers can be designed around the SCAR, and then re-amplified to look for fragment length polymorphisms on an agarose gel. Interestingly, this method is often used in combination with anonymous, dominant markers such as AFLPs and RAPDs, thereby also extending their utility.

An alternative, non-PCR-based marker method that is sometimes used by molecular ecologists is allozyme analysis. These markers are derived from loci encoding enzymes used in important metabolic processes (e.g., glycolysis). Although they are not as rapidly evolving as STS markers, they often yield moderate to high levels of genetic variation, depending on the organism. In either case, information from STS or allozyme markers can be used to determine if heterozygosity within populations is correlated with some ecological variable. For example, one could examine levels of heterozygosity relative to growth rate and performance in plants or adaptive response to environmental change in animals.
A third class of markers often used by molecular ecologists are those derived from direct DNA sequencing of targeted regions within the genome. These are often called Sanger sequencing (Figure 5). As with STS markers, DNA sequencing requires precise knowledge of specific genes, or gene regions, that are of interest to the investigator. Combined with PCR and well-designed primers, this method provides the finest and most fundamental level of genetic detail currently available to molecular ecologists. This is because the exact nucleotide sequence can be obtained for cross-comparison analysis of a wide range of taxonomic levels, from phyla to species, and, depending on levels of variation, even among individuals within a population. Thus, DNA sequencing is ideal for determining the evolutionary history of a group of organisms and for inferring evolutionary processes and patterns such as the genetic basis of adaptive trait loci (e.g., genes involved in responses to day length in plants), the historical patterns of migration and expansion of animal species (e.g., from the Pleistocene to present day), and the evolution of specific traits involved in taxonomic diversification (e.g., the origin of a notochord leading to vertebrates) — to name only a few. One particularly useful genome that has been used extensively by molecular ecologists studying animal phylogenetics is the organelar genome of mitochondrial DNA (mtDNA). One region of mtDNA that has proven especially informative at low taxonomic levels (i.e., species level) is the cytochrome oxidase I (COI) region, also known as the "bar-coding" region because of its ability to use universal primers and genetically barcode groups of diverse species. Another genome frequently used by plant molecular ecologists is the chloroplast genome, which has been used extensively to track historical patterns of plant migration and reconstruct plant phylogenies.

DNA sequencing has also enabled the development of another highly polymorphic, codominant marker type called single nucleotide polymorphisms (SNPs). When multiple sequences of a particular region are generated for multiple members within a species, single base differences among individuals are often detected. Depending on the level of DNA sequencing (e.g., individual regions v. whole genomes), SNPs can provide broad genome coverage, show high levels of variability, and can be used for phylogenetic reconstruction because the homology of these markers is known.

Another different but related approach to targeting individual gene regions is whole genome sequencing. One recently developed method that rapidly generates short sequenced segments that can be analyzed and compiled into whole genomes is called Next Generation Sequencing. Although typically limited to organisms with small genomes (e.g., bacteria or viruses), Next Generation Sequencing is becoming an important tool for molecular ecologists interested in probing entire genomes for clues to ecologically-based questions.

Given the strengths and weaknesses of different molecular genetic techniques, one might wonder how best to design an experiment for answering a particular ecological question. This subject requires careful consideration of both marker method and marker information content.

**Experimental Design: From Random Molecules to Appropriate Methods**

A key question to ask when employing genetic techniques is: Which one is best suited for my particular question? The answer to this question will be determined by several factors, all of which must be evaluated both individually and together in order to arrive at a cohesive plan for launching a successful molecular ecology study. Figure 6 shows a flow diagram for initial consideration of which method (or methods) best apply to your particular question. Although there are many different ways to approach this question, one simple strategy is to begin with the taxonomic level of investigation.
Are you interested in population-level differences within species? Are anonymous markers the only ones available for your organism of interest? If so, then AFLPs might be the marker of choice.

Do you need to know details such as observed or expected heterozygosity? Or, are you trying to correlate neutral marker variation (i.e., ones that are not under selection) with some environmental variable? In this case, AFLPs might be useful, but STS or allozyme markers might be a better way to go.

Are you interested in reconstructing the evolutionary history of a group of organisms? If so, at what level of inquiry is your question aimed: among species within genera, among genera, or at higher taxonomic levels (e.g., families, even phyla)? Depending on the region you intend to target (e.g., coding v. non-coding DNA, nuclear v. organelar mtDNA), homologous markers derived from DNA sequencing will likely provide the greatest dividends.

Do your interests revolve around genome evolution? For example, you might be interested in understanding how the genomes of pathogenic v. non-pathogenic bacteria differ and whether there are ecological or environmental correlates to the virulence of pathogen-related genes.

In this case, whole genome sequencing (not just individual gene regions), which is now feasible and can be easily used to analyze small genomes, would provide a rich source of information for the question of interest.

Although there are multiple ways to assess which marker is best for which question, thinking carefully about what levels of genetic variation you need and at which taxonomic level is paramount to choose the best approach. Understanding this very simple strategy and applying it thoughtfully can ultimately determine the degree to which your question is both answerable and publishable within the field of molecular ecology.
How Do Potential Competitors Partition Resources in Nature?

Careful and detailed study has revealed some of the many ways in which potential competitors show differences in patterns of resource use. Perhaps the most obvious way that species can partition resources is in terms of what they consume. This is often underpinned by differences in their morphological adaptations that allow differential resource use. For example, a detailed study of bumblebees in the mountains of Colorado (Figure 1) neatly shows how different species can be best adapted to specific forms of a resource (Pyke 1982). Bumblebee species all compete for nectar from flowers, but crucially these flowers vary in the length of their corolla. Matching this variation, different bumblebees in this area appear to be adapted to different species of plant that have different corolla lengths in their flowers. Careful observations of bumblebee visits to different flowers revealed clear resource partitioning — different species preferred different length corollas in accordance with their proboscis length (i.e., long proboscis, long corolla; short proboscis, short corolla).
Ecologists have found it relatively easy to document the various differences in the ways that ecologically similar animal species use their environment and resources. In many cases nothing more than a pair of binoculars and careful observation is required. Studying resource partitioning in plants can be much more challenging, and the relative lack of such examples has led many ecologists to wonder whether plants really do show resource partitioning; after all, they all require a limited suite of resources (light, water, and nutrients). However, ecologists do not give up easily, and recent work has shown that coexisting plant species often differ in the forms of nitrogen (e.g., ammonium versus nitrate or organic v. inorganic) they prefer (Kahmen et al. 2006). Differences in rooting depth and light-use optima have also been documented. Nevertheless, how common or important resource partitioning is in plants remains uncertain and is an active area of current research.

**Figure 1:** Resource partitioning among bumble bees (Bombus spp.)
Species have proboscises of different lengths, enabling them to specialize in the exploitation of plants with different length corollas. Species with similar length proboscises occur at different altitudes (Pyke 1982).

© 2011 Nature Education Adapted from Begon et al. (1990). All rights reserved.

**Same Slice, Different Restaurant**

When species use a resource similarly in one respect (i.e., they show "overlap" in their use of a resource along one axis), they commonly show differences in some other respect (along another axis). For example, the bumblebee study mentioned above was conducted over sites varying in altitude. Pyke (1982), the author of this work, found that although several bumblebee species had similarly long proboscises and so could forage on similar species of plant, they were differentially specialized to altitude, so that sites at different altitudes were dominated by a different pair of long- and short-length proboscis species. Another striking example comes from tree-dwelling Anolis lizards on the Caribbean island of Bimini (Schoener 1974; Figure 2). In this case, species either foraged in the same places (as determined by the thickness of branches they perched on) or ate similar sized prey, but in no cases did two species do both of these. In contrast, individuals of the same species commonly showed a high degree of overlap along both of these resource axes (Figure 2).

**Figure 2:** Similarity in structural habitat and prey size in pairs of individual Anolis lizards from the Caribbean island of Bimini
Pairs of classes that do not belong to the same species (interspecific) do not show high overlap along both axes (i.e., there are no interspecific pairs in the dashed box).

© 2011 Nature Education Adapted from Schoener (1974). All rights reserved.

**Is Resource Partitioning a Solution for Coexistence?**

Ecological theory shows that interspecific competition will be less likely to result in competitive exclusion if it is weaker than intraspecific competition (Chesson 2000). Resource partitioning can result in exactly this! By consuming slightly different forms of a limiting resource or using the same limiting resource at a different place or time, individuals of different species compete less with one another (interspecific competition) than individuals of the same species (intraspecific competition). Species, therefore, limit their own population growth more than they limit that of potential competitors, and resource partitioning acts to promote the long-term coexistence of competing species. Other theories have been put forward that attempt to explain the coexistence of large numbers of species in local communities, and assessing their importance relative to resource partitioning is likely to be an active
area of research for years to come. There is no doubt, however, that mechanisms reducing interspecific relative to intraspecific competition act to promote coexistence, and resource partitioning can achieve this.

**Competition Can Drive the Evolution of Differences**

So far we have discussed the phenomenon of resource partitioning and its role in reducing interspecific competition and therefore promoting coexistence. Where does resource partitioning come from in the first place (i.e., what causes species to be able to partition resources)?

Competition can limit the growth, and ultimately the reproductive success, of individuals. It can consequently serve as a selection pressure driving differential reproductive success and the evolution of traits that enable organisms to use resources differently compared to their competitors. This process has been clearly demonstrated in the evolutionary events that have followed the colonization of volcanic islands. For example, a single species of seed-eating finch originally colonized the Galapagos Islands and was faced with a diverse range of seed types and sizes. However, the beak of the founding species only allowed it to eat a small subset of the available seed types and sizes. The advantages gained by individuals that were able to exploit slightly different seed types drove evolution of many new species, each with different shaped beaks enabling them to specialize in a particular size of seed (Grant 1986).

There is convincing evidence that competition (and not another selection pressure such as predation) drove — and maintains — differences in beak sizes between these species. When species occur on their own on an island (i.e., there is no interspecific competition), they have similarly sized beaks and presumably exploit similarly sized seeds. When several species occur on the same island however, they show clear differences in beak shapes, showing that it is interspecific competition that maintains differences between species and resultant resource partitioning (Figure 3).

An interesting new twist has been added to this story of the evolution of resource partitioning. Around 25 years ago the island of Daphne Major, originally host to just a single species of Darwin's finch (Geospiza fortis) was invaded by another, larger beaked species (G. magnirostris). Amazingly, researchers have documented a rapid evolutionary shift in the sizes of beaks in G. fortis. In response to severe competition for larger seeds it has evolved to take full advantage of small seeds. This study is particularly important because the researchers were able to document the process of character displacement, and by monitoring the levels of resources, show that competition was the most likely possible cause (Grant & Grant 2006).

![Character Displacement](image)

**Figure 3: A classic example of character displacement**

When multiple species of Darwin's finches co-occur on an island, they show differences in bill depth (and eat different sized seeds) compared to when they are alone on an island.

© 2011 Nature Education Adapted from Morin (1999). All rights reserved.

**Resource Partitioning, Species Extinction, and the Functioning of Ecosystems**

Humans are causing widespread extinctions of species on local and even global scales. Recently, ecologists have realized that resource partitioning may have important implications for our understanding of the effects of losing species on the functioning of entire ecosystems.

Groups of ecologically similar species may all contribute toward the same, aggregate ecological processes; for example, grasses in a meadow all contribute towards overall primary production and predatory spiders in the same meadow may all contribute towards the control of plant herbivores. Maintenance of such ecological processes is important for the overall functioning of ecosystems, including ecosystem services that humans benefit from.

Resource partitioning can help scientists understand how aggregate ecological processes will be impacted by species extinction. If species show a high degree of resource partitioning, when a species is lost so too is the capacity of the ecological group to exploit the particular slice of the resource pie that the deleted species was adapted to exploit. For example, extinction of a species of grass that was uniquely specialized to use ammonium as a source of nitrogen would leave ammonium in the soil unused. Because this slice (ammonium) of the resource pie will not be exploited, the overall rate of new growth of meadow grass (primary production), as well as associated processes like uptake of carbon dioxide and production of oxygen, will be reduced.

A vast number of recent experiments show that species extinction, on average, reduces levels of ecosystem processes (Cardinale et al. 2006). Resource partitioning is thought to play an important role in causing this effect, although ecologists are only just beginning to directly test this (Griffin et al. 2008, Finke & Snyder 2008). There is an important application of this ongoing work — by considering the degree of resource partitioning among species scientists may be able to predict those ecosystems that are most vulnerable to the loss of species.
Summary
The long-term coexistence of ecologically similar species, and thus the astounding diversity of life on Earth, has long fascinated ecologists. Resource partitioning may hold the answer to the coexistence of species that make a living in similar ways (i.e., species are able to "stay out of the way of each other" and reduce interspecific competition by using resources differently). Indeed, the benefit of tapping into resources that another competing species cannot use as effectively can be so great that following the addition of a competitor, new traits can literally evolve right in front of the eyes of scientists!

The astounding diversity of species on Earth is at least partly attributable to the various ways in which potentially competing species have evolved specialized traits and intricately partitioned resource exploitation. Ecologists are beginning to realize that the very resource partitioning that helps maintain species diversity may also leave the overall functioning of ecosystems highly sensitive to species extinction.

References and Recommended Reading


Explore This Topic

OUTLINE | Keywords FEEDBACK

BASIC
Evolution Is Change in the Inherited Traits of a Population through Successive Generations
The Hardy-Weinberg Principle
Using Molecular Techniques to Answer Ecological Questions
Mutations Are the Raw Materials of Evolution

ADVANCED
Avian Egg Coloration and Visual Ecology
The Ecology of Avian Brood Parasitism
The Geography and Ecology of Diversification in Neotropical Freshwaters
The Maintenance of Species Diversity
Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations
Neutral Theory of Species Diversity
Population Genomics
Semelparity and Iteroparity

INTERMEDIATE
Why Are Life Histories So Variable?
Comparative Genomics
Case Study: The Glorious, Golden, and Gigantic Quaking Aspen
Cybertaxonomy and Ecology
Molecular Genetic Techniques and Markers for Ecological Research
Resource Partitioning and Why It Matters
Birds and humans perceive colors differently, so scientists rely on instruments and genetics to accurately describe the diversity of avian color signals.

Evolutionary processes have generated diverse color patterns of avian feathers, skin patches, and egg shells, which perform countless functions, including mimicry, crypsis, prey detection, predator avoidance, and signaling individual identity or mate quality (Hill & McGraw 2006). If color patterns function to communicate information, then do we need to understand the sensory and perceptual systems responsible for detecting these complex patterns? Recent technological and theoretical efforts have revolutionized the study of avian vision so that we now can use genetic sequencing of the opsin genes involved in avian color vision to reconstruct light-receptor sensitivity parameters, and this information can be used in perceptual models of birds’ vision. Combined, these two approaches allow for a better understanding of the role that visual ecology plays in the evolution of avian communication and recognition systems, especially in the study of egg mimicry, ultraviolet (UV) light sensitivity, and their role in shaping the sensory ecology and behavioral patterns of diverse bird species (Hubbard et al. 2010).

The Evolution of Egg Color Patterns

Why do bird eggs range in color from uniformly white to brightly colored and/or densely speckled (maculated; see Banner photo)? Based on a comparison of eggshell patterns between different avian families, one of the most prevalent ecological factors responsible for the diversity of egg coloration is the interaction between brood parasites and their hosts (Kilner 2006). Obligate brood parasitic birds lay their eggs in nests of other species, thereby imposing a cost on hosts to raise genetically unrelated young (Davies 2000). Egg coloration and maculation play important roles in whether hosts accept or reject the fitness costs imposed by parasitism. For example, the blackcap (Sylvia atricapilla) is a host of the parasitic common cuckoo (Cuculus canorus) in Europe and typically rejects all non-mimetic (dissimilar) eggs (Honza et al. 2004). By experimentally parasitizing blackcap nests with host-like mimetic eggs (using eggs of other blackcaps), egg rejection drops to 36% (Polacikova et al. 2007). Accurate rejection of foreign eggs even at seemingly low rates can still be an adaptive behavior because the host reduces its chances of spending time and energy raising overly needy and genetically unrelated offspring.

These and other cuckoo hosts appear to have evolved a simple rule of thumb to direct their behavior: “eject the egg unlike your own”. But how does a bird know what its own eggs look like? Researchers have tackled this question by experimentally manipulating the appearance of the bird’s own egg by dying one, more, or all eggs in the same brood (Figure 1). Such studies reveal that great reed warbler (Acrocephalus arundinaceus) hosts rely on both color differences between eggs and learned memories of their own eggs to recognize and reject cuckoo eggs (Moskát et al. 2010).
Figure 1: Dyeing birds’ own eggs (here in the nest of the song thrush Turdus philomelos) allows for an experimental manipulation of (a) color and/or (b) maculation, without the confounds of changing size, shape, or eggshell thickness, to assess the role of visual ecology in discriminating own and foreign eggs. The photo on the left shows an experimentally darkened song thrush egg among unmarked eggs. The photo on the right shows two song thrush eggs whose spots have been experimentally expanded next to an unmarked egg. © 2010 Nature Education Courtesy of M. Hauber. All rights reserved.

Truly astounding, though, is that selection for visual cues of recognition has resulted in the evolution of extreme level of egg color mimicry of specific hosts by different parasitic cuckoos (Figure 2). Through the process of coevolutionary arms race, egg mimicry also has likely influenced the perceptual sensitivities of hosts and their abilities to correctly identify and reject foreign eggs from the nest. The perceptual acuity necessary to make a correct rejection invites direct investigation; researchers can experimentally parasitize the nests of hosts with eggs of varying degrees of similarity, in order to determine the thresholds in color and maculation at which hosts make decisions to reject dissimilar, and likely foreign, eggs from their nest.

Figure 2: Nests with both host and parasitic common cuckoo eggs, illustrating near-perfect mimicry to the human eye. Black arrows identify cuckoo egg. © 2010 Nature Education Courtesy of M. Honza, T. Grim, & C. Moskat. All rights reserved.

Avian Color Perception

Before an experimenter can set out to manipulate egg colors, especially the ones hypothesized to be important for foreign egg rejection, it must be first established which colors that host species can see. The cone photoreceptors of the vertebrate retina (Figure 3) are responsible for color vision. The genes for opsins encode specific photopigments expressed in these cones, generating different combinations of proteins with maximal sensitivities to a particular wavelength of light (\(\lambda_{\text{max}}\)). The cone cells of all color-sensitive vertebrates express opsins. The number of different opsins that an individual possesses is related to the number of colors to which it is sensitive.
Avian retinas differ from those of mammals in many ways, notably in the number of cone types that they possess. Unlike mammals, which typically have only two or three different cone types (Figure 4), bird species possess 4 distinct single cone types in their retinas, making them tetrachromatic (Figure 5; Hunt et al. 2009). Tetrachromats are theoretically able to see twice as many colors as trichromats (e.g., humans). For example, two eggs might appear indistinguishable to us, but a bird might see them displaying two distinct colors. This has direct implications for scientific investigations of avian perception — how can we manipulate egg colors when birds themselves may be more sensitive than we are to subtle differences in color?

Figure 3: Schematic diagram of the mammalian retina.
Public Domain WikiMedia Commons.

Figure 4: Differences in wavelengths of maximum absorbance of the three cone opsins (S, M, and L) and rhodopsin (R) in the human retina.
Public Domain WikiMedia Commons.

Some avian lineages, including many passerines, are able to see light in the ultraviolet (UV) range, which humans cannot see (Hart 2001). The hosts of brood-parasitic cuckoos in Europe and brown-headed cowbirds (Molothrus ater) in North America are passerines, implying that they might be able to perceive cryptic (to human) UV differences between their own and parasitic eggs to discriminate and reject parasitic eggs. One of the types of opsins (SWS1) is sensitive to the shortest wavelengths of light, and is found in all vertebrate classes (Hazel et al. 2006). In humans and many bird species, the SWS1 opsin is expressed in cones that respond maximally to violet light (such species are termed violet-sensitive, VS). In some passerine species, however, the SWS1 opsin gene codes for a photoreceptor with a $\lambda_{\text{max}}$ that crosses into the UV portion of the light spectrum (Figure 6). Species with this type of SWS1 cone are UV-sensitive (UVS; Hart 2001; Ödeen & Håstad 2003; Hunt et al. 2009).
A UV-sensitive SWS1 is apparently ancestral among vertebrates, but was subsequently lost in primates and birds (Yokoyama 2000; Jacobs & Rowe 2004; this is a great review for those interested in the evolution of color vision in vertebrates). Among birds, however, UVS has re-evolved independently at least 4 times via a shift in SWS1 sensitivity (Hunt et al. 2009). UV-sensitivity in turn can serve a number of adaptive behavioral and ecological functions, including sexual displays, predator/prey detection, intraspecific communication to avoid detection by VS predators (Håstad et al. 2005), and defense mechanisms against egg mimicry in brood parasitism (Honzà et al. 2007; Underwood & Sealy 2008). These two latter studies demonstrate that the UV-reflectance of eggs differs between host and parasite, suggesting that hosts can use UV-only visible patterns to discriminate between their own and foreign eggs. Whether UV-sensitivity evolved as a response to brood parasitism or was already available for hosts to utilize at the onset of their evolutionary history with brood parasitism, remains still unknown (Underwood & Sealy 2008).

Regarding other ecological contexts, eggs of cavity-nesting species tend to have higher UV-reflectance than eggs of open cup nesters (Aviles et al. 2006), providing further evidence that UV light can both be seen and be informative for parental birds’ behavioral decisions. Accordingly, cavity-nesting spotless starlings (Sturnus unicolor) are more likely to accept experimental eggs placed just outside the nest cup within the cavity (by pulling them them into the nest) with high UV-reflectance than eggs with low UV-reflectance.

But how can we know whether the SWS1 opsin of a particular bird species will be maximally sensitive to UV or violet wavelengths of light? Much of our knowledge of the avian sensory world now derives from physiological and molecular techniques which describe the sensitivities of opsins present in the eye. The traditional method of microspectrophotometry allowed researchers to determine the $\lambda_{\text{max}}$ of any photoreceptor by transmitting light through it and measuring which wavelengths are absorbed (Gavardovský et al. 2000). More recently, DNA sequencing of the SWS1 opsin gene has allowed researchers to assign VS/UVS states in a more cost-effective and non-lethal manner, relevant for large scale comparative studies (Ödeen & Håstad 2003), including work with bird species of conservation concern for which invasive studies cannot be done (Igic et al. 2010).

The molecular machinery of the SWS1 photoreceptor requires only one amino acid substitution in a select few sites of the protein’s amino-acid chain to change a VS species or individual to a UVS species or individual (Yokoyama 2000). Genetic sequencing of the SWS1 opsin gene is now regarded as an accurate, reliable and economical alternative to microspectrophotometry (but see Smith et al. 2002).

Perceptual Modeling of the Avian Visual System

Integrative research spanning the fields of molecular genetics, physical light reflectance measurements, and behavioral experiments, has allowed researchers to quantify color patterns as birds would see and use them (Vorobyev & Osorio 1998; Ender & Mielke 2005). To interpret physiological and genetic data, however, requires perceptual models which are mathematical representations of what a bird can see, based on a number of different parameters, including the amount of light that reaches the retina and the relative abundance and type of photoreceptors present in that particular species’ eyes. Using physiological data generated from genetic sequencing of the opsin genes (Ödeen & Håstad 2003), researchers can now produce reasonably accurate models of avian visual perception and its behavioral implications in egg rejection decisions (Cassey et al. 2008). Typically, the light reflectance of surfaces of interest, such as eggshells, is measured with a spectrophotometer and the resulting relative light reflectance data are then filtered through the perceptual model’s equations to assess whether a species in question can see differences between particular light reflectance patterns, or colors.

Color Vision Links Sensory Ecology with Behavioral Decisions

Perceptual modeling has been adapted to study a wide range of phenomena; these include the perceived variability in eggshell colorations across many bird species (e.g. Cassey et al. 2009; Cassey et al. 2010), the adaptive use of human-made refuse as nesting material (Igic et al. 2009), as well as sexual dimorphism (Igic et al. 2010). Future studies of perceptual modeling should focus on the differences in egg colors between brood parasites and their hosts, and whether or not hosts are visually equipped to perceive these differences. Overall, molecular techniques and sensory modeling now allow researchers to begin to study the mechanisms underlying avian color vision, and do not require severely invasive methods. These integrative approaches make it possible for future researchers to accurately describe and manipulate salient color information in studies of mimicry, crypsis, mate quality, and other behavioral functions critical for survival and reproduction across diverse species of birds and other visually oriented animal lineages.

References and Recommended Reading


Figure 5: Differences in wavelength of maximum absorbance between species possessing the UVS v. the VS SWS1 opsin photoreceptor

© 2010 Nature Education All rights reserved.


The Ecology of Avian Brood Parasitism

By: Rebecca Croston (Biology Program at the Graduate Center, CUNY) & Mark E. Hauber (Dept. of Psychology at Hunter College, CUNY) © 2010 Nature Education

The Ecology of Avian Brood Parasitism

Brood parasitic birds lay their eggs in the nests of others, sparing themselves the expense of rearing their own young. The resulting coevolutionary arms race includes sophisticated defenses by hosts and escalating tools of exploitation by parasites.

Brood Parasitism as a Reproductive Strategy

Avian brood parasitism, or the laying of one’s eggs in the nest of another individual, is a reproductive strategy whereby parasites foist the cost of rearing their offspring onto another individual, the host (Davies 2000). Brood parasitism may be facultative at the species or individual levels, with some eggs incubated by the mother and others laid in foreign nests, or obligate. Brood parasitism may also be intraspecific, with eggs laid in other nests of the parasite’s own species, or interspecific, with all eggs laid in the nests of other species. Cowbirds and cuckoos are the most commonly studied avian brood parasites (Davies 2000), although obligate interspecific brood parasitism has evolved at least 7 separate times among various avian clades, including cowbirds (Icteridae), honeyguides (Indicatoridae), Old World cuckoos (Cuculinae), twice in the New World cuckoos (Neomorphinae), andigobirds and their allies (Ploceidae), and the Black-headed duck (Anatidae).

For the parasite, benefits include increased fecundity due to greater allocation of resources toward mating and producing more eggs rather than defending nests, incubating eggs, and feeding young. For hosts of brood parasitic birds, the costs of parasitism range from diminished nestling growth rate, due to competition with larger and more competitive parasitic offspring (cowbirds, whydahs), to total loss of breeding by the abandonment of parasitized broods (cowbirds, cuckoos), or the killing of host hatchlings by parasitic hatchlings (cuckoos, honeyguides) (Kilner 2005; Servedio & Hauber 2006). These costs exert reciprocal natural selection on parasites and hosts, such that in many cases host-parasite interactions result in escalating coevolution between intimately tied and interdependent species (Langmore et al. 2003). In turn, many hosts are able to discriminate against and reject foreign eggs or chicks based on visual, acoustic, or multimodal sensory cues (Cassey et al., 2008). The eggs of many brood parasites, for example, mimic those of their hosts (to deceive hosts to accept), have harder shells (to impede rejection by puncture), and require slightly shorter incubation times (causing a size advantage for parasitic nestlings) (Davies 2000) (Figure 1).
Evolution and Maintenance

There are two major hypotheses that have been implemented in attempting to explain the evolution and maintenance of the complex and often paradoxical reproductive strategies that fall under brood parasitism (Rothstein & Robinson, 1998). The evolutionary lag hypothesis posits that rejection is almost always more adaptive than acceptance, so that 1. hosts accept parasitism only because they have not yet evolved mechanisms for defense against parasites and/or 2. parasites fail with certain hosts because they have not yet evolved mechanisms for overcoming existing host defenses. Historically recent contact, due to natural or anthropogenic change (e.g., deforestation, forest fragmentation), the acceptance of foreign eggs even when these do not resemble host eggs (nonmimetic), and a high cost of parasitism without apparent defenses to prevent and recognize parasitism, all suggest that evolutionary lag is the mechanism for host acceptance of parasitic eggs, but as it is difficult to test this hypothesis directly, it is often the default or fall-back explanation (Peer & Sealy 2004).

In contrast, the evolutionary equilibrium hypothesis posits that hosts accept parasitism only because the cost associated with the rejection of parasitic eggs is greater than the cost of rearing cowbird offspring (Klippenstine & Sealy 2008). Rejection costs may be incurred via misrecognition of parasitic eggs, so that hosts mistakenly eject their own eggs, or via rejection costs, when hosts accidentally damage their own eggs while attempting to remove parasitic eggs. Host-egg mimicry and increased eggshell thickness by parasitic eggs have both evolved repeatedly in diverse lineages of obligate parasites, rendering the recognition and removal of parasitic eggs more costly, and thereby increasing selective pressure to accept parasitism or delay the evolution of costly and error-prone discrimination mechanisms to reject parasites.

The Coevolutionary "Arms-Race"

Egg Mimicry

Most host defenses against costly parasitism occur at the egg stage with the recognition and removal of parasitic eggs. This ability may have evolved from behaviors such as nest sanitation (removal of fecal sacs and broken shells), and morphological traits such as large bills, which serve as preadaptations for removal of parasitic eggs (Peer & Sealy 2004). Egg recognition thereby exerts selective pressure on the parasites to lay eggs that mimic in appearance those of their host, and reciprocal pressure on hosts to fine-tune their discriminative abilities. This "arms race" is at the heart of brood parasitism as a coevolutionary phenomenon. The degree of egg mimicry and concurrent host specialization varies dramatically among parasitic clades. A recent study by Klippenstine and Sealy (2008) has shown that grassland cowbird hosts possess the ability to discriminate between and reject foreign eggs when the eggs differ dramatically (in color and maculation) from their own eggs, but those same species do not eject real or model cowbird eggs. This suggests that a more generalized form of egg mimicry than that employed by cuckoos, and that Brown-headed cowbirds (Molothrus ater) eggs loosely mimic a wide range of potential grassland hosts. In contrast, individual females of many old world cuckoos, lay eggs that are specific to particular hosts — that is, they mimic eggs of a specific subset of their host species. Generalist cowbirds, by contrast, do not lay highly mimetic eggs, and parasitize a wide range of hosts rather than specializing on a particular species of host or host-egg race. Recognition and removal of parasitic eggs is based largely on differences between own and foreign eggs in background color, with size, shape, and maculation varying in various combinations to elicit egg rejection. A major caveat in studies of degree of egg color matching to date has been that eggs are assessed according to the human visual system. As many birds possess a fourth, UV-sensitive photoreceptor type relevant in behavioral decision-making, biologically realistic sensory models should be used in future studies to determine the parameters eliciting egg rejection (Cassey et al. 2008; Honza et al. 2017).

Nestling Mimicry

If constraints surrounding egg recognition and removal make rejection at the egg stage too costly, the recognition and rejection of nestlings may provide an effective alternative defense strategy for host species, ultimately resulting in plumage, mouth, and begging call mimicry (Langmore et al. 2003; Anderson et al. 2009). For post-hatching discrimination to evolve, parasitism rates must be sufficiently high to outweigh the cost of recognition errors, and hosts must have sufficiently high fecundity to bear the cost of mistakenly rejecting their own chicks (Langmore et al. 2003). Host rejection of parasitic nestlings has been demonstrated in Superb Fairy-wrens (Malurus cyaneus), and may have selected for the evolution of nestling begging call mimicry in Housefield's Bronze-Cuckoo (Chalcites basalis) (Langmore et al. 2003). Nestling discrimination by hosts is, however, relatively rare, despite hosts having various behavioral and cognitive traits that would enable such behavior. This is likely because nestling discrimination can only evolve when egg discrimination has failed (Grinn 2006).

Hosts may discriminate nestlings using cues such as size, color, vocalization, and overall clutch size. Mouth coloration and gape patterns of parasitic nestlings can stimulate higher rates of provisioning by host parents as a supernormal stimulus and enabling parasites to outcompete host...
young (Kilner et al. 1999). In parasitic indigobirds, nestling flange markings may resemble those of healthy hosts in order to stimulate greater provisioning (Hauber & Kilner 2007) and to avoid discrimination through reduced feeding by host parents (Schuetz 2005).

**Identity Crisis?**
If parasitic nestlings are not exposed to conspecifics during development, then how are they able to identify members of their own species with which to mate? Rather than relying solely on cues learned from parents and nestmates, brood parasites must employ some other mechanism for species recognition in order to avoid mistakenly courting heterospecifics. Brownheaded Cowbirds seem to rely on a combination of self-referent phenotype matching and a “password” like vocal trigger that unlocks learning of species-specific cues at their first encounter with a conspecific (Hauber & Sealy 2000, 2001). Such a combination of developmental paths and recognition mechanism may apply to brood parasites more generally, and could represent a difficult-to-evolve behavioral algorithm, as was seen recently in an experimental study where male facultative interspecific brood parasitic ducks mistakenly courted females of the host species instead of their own (Sorenson et al. 2010).

**Conservation Impacts of Brood Parasitism**
As a widespread generalist brood parasite, the native Brown-headed Cowbird poses a conservation threat to several of its North American passerine hosts. Selective pressure resulting from cowbird parasitism is likely higher now than in the past, owing to increased suitable habitat provided by deforestation, leaving more and new host species vulnerable to parasitism by increasing numbers of cowbirds (Davis & Sealy 2000). For brown-headed cowbird host populations already in decline, such as the endangered Kirtland's Warblers (Dendroica kirtlandii), Black-capped Vireos (Vireo atricapilla), Leasi Bell's Vireos (Vireo bellii pusillus), and Southwestern Willow Flycatchers (Empidonax insulorum), the effects of this can be devastating, and human control of cowbird population size may be necessary to prevent local extinctions (Smith et al. 2000). This is a particular consideration for conservation biologists working with hosts of generalist brood parasites, because even when a species declines in number it may continue to be parasitized at high rates, since as generalist parasites, the cowbird population will not be impacted reciprocally with that of individual host species. These applied aspects of host-parasite interactions confirm that scientifically informed conservation management is critical for the efficient and productive planning and implementation of long term goals (Hauber 2009; Parker et al. 2010).

**References and Recommended Reading**

Explore This Topic
The Geography and Ecology of Diversification in Neotropical Freshwaters

By: James S. Albert (University of Louisiana at Lafayette) & William G. R. Crampton (University of Central Florida) © 2010 Nature Education


This article addresses central themes in the study of tropical biodiversity, exploring the roles that speciation, extinction, and dispersal play in the formation of regional assemblages.

The unparalleled diversity of tropical ecosystems has drawn the attention of naturalists since the earliest voyages of discovery in the eighteenth and nineteenth centuries. The fundamental question then, as now, is: Why so many species? One influential perspective seeks to explain species richness at the community level in terms of mechanisms for ecological coexistence (Gause 1934, Hutchinson 1957). The central idea is that each species occupies a unique ecological niche, a distinct functional role within the ecosystem (Darwin 1859). Under this view species richness arises from the actions of natural selection to reduce competition or increase adaptive specialization.

Another view stresses the importance of historical or phylogenetic aspects of species diversification (Whittaker 1972). For example, the "species-pool" hypothesis describes local diversity by reference to the size (species richness) of the regional or global pool of species from which the local assemblage may be recruited (Taylor et al. 1999). From a macroevolutionary perspective, net rates of diversification within a geographic region arise from differential rates of speciation, extinction, and immigration (Rosenwag 1995, Stanley 1998, Jablonski 2000). Although the mechanisms of these processes remain incompletely understood for most biotas, we have known for at least a century and a half that evolutionary diversification takes place both in space and time. Biodiversity, biogeography, and paleontology are therefore all intimately related subjects.

Exceptional Amazonia

Amazonia exhibits all the principle features associated with aquatic species richness globally (Albert & Reis 2011). It is the greatest interconnected fluvial system on the planet, extending over more than seven million km². The Amazon River alone carries about a sixth of the all world's flowing freshwater. Its tropical location, straddling the equator, means it receives high levels of solar radiation and precipitation, and the region is largely covered by humid lowland rainforests. From a purely ecological perspective, therefore, Amazonia as it exists today appears to be an excellent environment for diversification in fishes.

Yet the species-rich Amazonian ichthyofauna is ancient and did not arise under the geological conditions of the modern Amazon Basin (Lundberg et al. 2010). Direct fossil evidence shows that many phenotypes and lineages date to the early Neogene or Paleogene (16 to 65 million years ago; Ma), before the Amazon assumed its modern courses. For example, the Amazon River only adopted its current east-flowing course after about 11 Ma; prior to this it flowed west and north into the Caribbean (Figueroa et al. 2009).

Furthermore, data from species-level phylogenetic and biogeographic studies tell us that Amazonian ichthyofaunas accumulated incrementally over a period of tens of millions of years, principally by means of allopatric speciation, and in an arena extending over most of the area of tropical South America (Albert & Reis 2011). In other words, unlike some of the well-known insular faunas (Galapagos finches, Hawaiian drosophilid flies, African rift lake cichlids), the species-rich Amazonian ichthyofauna is not the result of recent adaptive radiations.

Vicariance and Geodispersal

The geological history of landscapes is tightly linked with the evolution of their resident biotas. For freshwater organisms, landscapes are divided naturally into discrete drainage basins by watersheds, episodically isolated and reunited by erosional hydrodynamics. In regions like the Amazon Basin with an exceptionally low (flat) topographic relief, the many waterways have had a highly reticulated history over geological time.

Stream capture is an important geographic factor affecting the evolution and distribution of freshwater organisms. Stream capture occurs when an upstream portion of one river drainage is diverted to the downstream portion of an adjacent basin. This can happen because of geophysical uplift (or subsidence), natural damming as a result of a landslide, or by headward or lateral erosion of the watershed between adjacent basins.

http://www.nature.com/scitable/knowled.../1/10/13
In tropical South America groups of closely related fish species usually exhibit a geographic barrier to dispersal and gene flow, which spatially isolates populations and may lead to the formation of new species (i.e., allopatric speciation; Figure 2). This contrasts with parapatric and sympatric models in which selection and ecology are necessarily involved in the formation of new species lineages. Geodispersal is the erosion of such barriers (e.g., the formation of portals, corridors or bridges between formerly isolated regions). A well-known instance of geodispersal was the Plio-Pleistocene rise of the Panamanian isthmus around 3 Ma that connected Central and South America and led to the Great American Biotic Interchange.

Permeability of Geographical Barriers

The emergence of large tectonic structures, like ocean basins and mountain chains, usually forms impermeable barriers to dispersal and gene flow. However, species-level phylogenies and distributions cannot be used to unambiguously prove a particular geographic mode of speciation (e.g., sympatric v. allopatric) because geographical ranges may change following speciation.

Stream capture also differentially affects taxa depending on their demographic susceptibilities to extinction. Populations isolated on either side of a newly-formed watershed are likely to have reduced population sizes, which may accelerate genetic divergence and speciation or lead to local extinction. Taxa with high riverine vagility may use the new connections to expand their ranges and avoid extinction. Such newly arrived exotics may also adversely affect members of the resident fauna. In this hypothetical example the newly diverged species at t3 may subsequently disperse throughout the Eastern basin (E). Stream capture also changes the total area of each basin, and by means of the species-area relationship, the rates of speciation and extinction. The area of the Western basin (W) decreases in area, and may therefore maintain fewer species over evolutionary time.

From a biogeographic perspective, stream capture almost always involves both vicariance and geodispersal (Figure 1). Vicariance is the emergence of geographic barriers to dispersal and gene flow, which spatially isolates populations and may lead to the formation of new species (i.e., allopatric speciation; Figure 2). This contrasts with parapatric and sympatric models in which selection and ecology are necessarily involved in the formation of new species lineages. Geodispersal is the erosion of such barriers (e.g., the formation of portals, corridors or bridges between formerly isolated regions). A well-known instance of geodispersal was the Plio-Pleistocene rise of the Panamanian isthmus around 3 Ma that connected Central and South America and led to the Great American Biotic Interchange.

Permeability of Geographical Barriers

The emergence of large tectonic structures, like ocean basins and mountain chains, usually forms impermeable barriers to dispersal and gene flow. However, species-level phylogenies and distributions cannot be used to unambiguously prove a particular geographic mode of speciation (e.g., sympatric v. allopatric) because geographical ranges may change following speciation.

Stream capture also differentially affects taxa depending on their demographic susceptibilities to extinction. Populations isolated on either side of a newly-formed watershed are likely to have reduced population sizes, which may accelerate genetic divergence and speciation or lead to local extinction. Taxa with high riverine vagility may use the new connections to expand their ranges and avoid extinction. Such newly arrived exotics may also adversely affect members of the resident fauna. Although the responses of individual taxa are varied, the response of a fauna as a whole to stream capture is likely to be increased rates of both speciation and extinction; in other words, increased rates of net diversification.

Permeability of Geographical Barriers

The emergence of large tectonic structures, like ocean basins and mountain chains, usually forms impermeable barriers to dispersal and gene flow. Many groups of plants and animals, including freshwater fishes, were permanently isolated on either side of the newly-formed Atlantic Ocean during the final separation of Africa from South America in the Upper Cretaceous (around 110 Ma). Similarly, the early Neogene (around 12 Ma) rise of the Eastern Cordillera of the northern Andes permanently separated lowland northern South America into taxonomically distinct cis- and trans-Andean biotas (Albert et al. 2006). Impermeable barriers such as these are often spatially expansive, affecting broad geographic areas and multiple phylogenetically independent clades. Impermeable barriers are therefore excellent systems to study the role of vicariance in the formation of regional biotas.

Yet tectonic activity is highly punctuated in time and space. Most mountain building in the Andes occurred in relatively discrete pulses lasting just 5–10 million years each, interrupted by much longer periods of tectonic quiescence. By contrast, most of lowland tropical South America has changed gradually through the perennial action of erosion. Stream capture results in subtle and complex patterns in the geographic separation and merging of river basins and freshwater biotas. As noted above, a single stream capture event has both vicariant and geodispersal effects, simultaneously isolating a headwater tributary from one basin and connecting it to that of an adjacent basin.

In tropical South America, with its flat topography and low-altitude watersheds, many basins boundaries have been semipermeable over geological time scales (Lovejoy et al. 2010a). Semipermeable watersheds are environmental filters in the sense that they allow differential dispersal among adjacent basins. Fish species with high vagility between basins are those able to inhabit small streams and seasonal wetlands of the intervening areas and to tolerate suboptimal environmental conditions (e.g., dysxia, variable temperatures). Species that are ecologically restricted to large lowland rivers and freshwater biotas. As noted above, a single stream capture event has both vicariant and geodispersal effects, simultaneously isolating a headwater tributary from one basin and connecting it to that of an adjacent basin.

Stream capture also differentially affects taxa depending on their demographic susceptibilities to extinction. Populations isolated on either side of a newly-formed watershed are likely to have reduced population sizes, which may accelerate genetic divergence and speciation or lead to local extinction. Taxa with high riverine vagility may use the new connections to expand their ranges and avoid extinction. Such newly arrived exotics may also adversely affect members of the resident fauna. Although the responses of individual taxa are varied, the response of a fauna as a whole to stream capture is likely to be increased rates of both speciation and extinction; in other words, increased rates of net diversification.

Phylogenetic and biogeographic patterns in the electric fish Gymnotus (Gymnotidae) illustrate how stream capture across low-elevation watersheds on the relatively flat South American platform contribute to elevated species richness of regional assemblages (Figure 3). The Neogene rise of the northern Andes resulted in relatively impermeable barriers to fish dispersal, isolating cis- and trans-Andean lineages in both the G. canapo and G. figue groups.
By contrast, most watersheds in lowland Amazonia are relatively more permeable, several of which are indicated by dashed gray bars in Figure 3. Due to post-speciation dispersal, the Gymnotus species of the Amazon basin do not form a monophyletic group but rather represent an assemblage of species with origins in several basins (Albert et al. 2004).

Figure 3: Effects of vicariance and geodispersal on the formation of regional assemblages
(A) Schematic phylogenies of two clades of the electric fish Gymnotus (Gymnotidae). Some species of the G. carapo group (in red) are omitted for clarity. Thick horizontal bars represent geographic barriers. Note polyphyletic origin of the Amazonian assemblage. (B) Paleogeographic vicariance and coupled geodispersal events used to constrain divergence times. Dates represent minimum lineage divergence time estimates in millions of years ago (Ma). Semipermeable watersheds are "leaky" and do not provide reliable minimum divergence times (i.e., dates for semipermeable barriers represent date ranges that extend to 0 Ma). Data from Lovejoy et al. (2010a, 2010b).

© 2010 Nature Education All rights reserved.

Phylogenetic Niche Conservatism

Phylogenetic and biogeographic patterns in Neotropical freshwater fishes suggest that most speciation has occurred along geographic, not ecological, lines. In most groups of Neotropical fishes, diversification occurred incrementally over large spatial and temporal scales, with speciation occurring over much of the continental platform and requiring tens of millions of years. Vicariance and geodispersal are complimentary biogeographic processes that have profoundly influenced the formation of new species and the taxonomic composition of regional biotas. Together these processes interact in a complex web of Earth history events and biological diversification. These results from Neotropical freshwater fishes support an emerging paradigm shift within the field of ecology: Geography and phylogenetic history play an immensely important role in the formation of local species assemblages.

Formation of Regional Assemblages

Phylogenetic and biogeographic patterns in Neotropical freshwater fishes suggest that most speciation has occurred along geographic, not ecological, lines. In most groups of Neotropical fishes, diversification occurred incrementally over large spatial and temporal scales, with speciation occurring over much of the continental platform and requiring tens of millions of years. Vicariance and geodispersal are complimentary biogeographic processes that have profoundly influenced the formation of new species and the taxonomic composition of regional biotas. Together these processes interact in a complex web of Earth history events and biological diversification. These results from Neotropical freshwater fishes support an emerging paradigm shift within the field of ecology: Geography and phylogenetic history play an immensely important role in the formation of local species assemblages.

Conclusion

Phylogenetic and biogeographic patterns in Neotropical freshwater fishes suggest that most speciation has occurred along geographic, not ecological, lines. In most groups of Neotropical fishes, diversification occurred incrementally over large spatial and temporal scales, with speciation occurring over much of the continental platform and requiring tens of millions of years. Vicariance and geodispersal are complimentary biogeographic processes that have profoundly influenced the formation of new species and the taxonomic composition of regional biotas. Together these processes interact in a complex web of Earth history events and biological diversification. These results from Neotropical freshwater fishes support an emerging paradigm shift within the field of ecology: Geography and phylogenetic history play an immensely important role in the formation of local species assemblages.

References and Recommended Reading


http://www.nature.com/scitable/knowled...
Evolution is change in the inherited traits of a population through successive generations.

The Hardy-Weinberg Principle

Using molecular techniques to answer ecological questions

Mutations are the raw materials of evolution

Avian egg coloration and visual ecology

The ecology of avian brood parasitism

The maintenance of species diversity

Natural selection, genetic drift, and gene flow do not act in isolation in natural populations

Neutral theory of species diversity

Population genomics

Semelparity and iteroparity

Why are life histories so variable?

Comparative genomics

Case study: The glorious, golden, and gigantic quaking aspen

Cybertaxonomy and ecology

Molecular genetic techniques and markers for ecological research

Resource partitioning and why it matters
The Maintenance of Species Diversity

By: Jonathan M. Levine (Department of Ecology, Evolution, and Marine Biology, University of California) & Janneke HilleRisLambers (University of Washington, Department of Biology) © 2010 Nature Education

Earth is home to an astonishing diversity of species that provide food, medicine and other infrastructure necessary for the existence of humankind. Given intense competition between species for limited resources, how is this diversity maintained? Ecologists have shown that differences in how species interact with their environment counter the inevitable loss of biodiversity that occurs when better competitors overrule their inferior counterparts.

The ecosystems of the world contain a remarkable diversity of species. An area of tropical rainforest the size of fifteen city blocks may contain over a thousand different tree species (Figure 1a, Kraft et al. 2008). As ecologists have found in a Panamanian rainforest, close examination of just one of these tree species can yield as many as 945 different species of beetles alone (Figure 1b, Erwin et al. 1980). This astonishing diversity also extends to aquatic environments. Africa’s Lake Malawi is home to over 500 species of fish belonging to a single genus (Figure 1c; Kornfield & Smith 2000). In fact, the number of species on Earth is so overwhelming that the 1.7 to 2 million species currently described by biologists (Millenium Ecosystem Assessment 2005) is likely to be only a small fraction of the true total.

This astonishing biodiversity is valued for many reasons. The crops and livestock we rely on for food are derived from wild species long ago domesticated, and future improvements to agricultural productivity and sustainability depend, to a large extent, on genes derived from wild rather than domesticated populations. From a human health perspective, a significant fraction of medicines prescribed today contain chemical compounds that were originally isolated from wild organisms, including aspirin (from willow trees), the cancer drug taxol (from yew trees), and penicillin (from a fungus). In addition, diverse habitats are increasingly understood to be more stable in their provisioning of ecosystem services including clean water and the pollination of agricultural crops (Millenium Ecosystem Assessment 2005).

This astonishing biodiversity is valued for many reasons. The crops and livestock we rely on for food are derived from wild species long ago domesticated, and future improvements to agricultural productivity and sustainability depend, to a large extent, on genes derived from wild rather than domesticated populations. From a human health perspective, a significant fraction of medicines prescribed today contain chemical compounds that were originally isolated from wild organisms, including aspirin (from willow trees), the cancer drug taxol (from yew trees), and penicillin (from a fungus). In addition, diverse habitats are increasingly understood to be more stable in their provisioning of ecosystem services including clean water and the pollination of agricultural crops (Millenium Ecosystem Assessment 2005).

Humankind derives tremendous benefits from the wide diversity of species on Earth, but this diversity also poses a fundamental ecological puzzle. Speciation, the evolutionary process by which new species are formed, is clearly responsible for the ultimate generation of species diversity over geologic time. But once generated, how is this diversity maintained? What prevents the single best competitor from displacing all other species? How different species coexist (co-occur in the same location for many generations) is a long-standing and not fully resolved question for ecologists (Gause 1932).
The mystery of species coexistence is rooted in the competitive exclusion principle, which states that two species competing for the same resource cannot coexist (Gause 1934, Hutchinson 1961). The species that is better at gaining the limiting resource will eventually eliminate the inferior competitor. This intuitive idea has been central to the field of ecology at least since Darwin’s exposition of his theory of evolution, but mathematical theory and laboratory experiments with single-celled organisms in the early part of the twentieth century reinforced this foundation (Gause 1934).

The simple prediction of the competitive exclusion principle is schematically portrayed in Figure 2a. If a superior and an inferior competitor are placed into a habitat at initially equal abundance, the former will inevitably eliminate the latter. Envision, for example, two rodent species, one that has a much greater ability than the other to consume seeds, the food resource limiting their growth. Eventually, the better seed competitor will win (the blue species in Figure 2a). The take home message is that differences in the competitive ability of different species cause their abundances to diverge over time, resulting in one species becoming more common while the other becomes less common (Gause 1934, Chesson 2000). If the differences in the competitive ability of species are large, the poorer competitor will be rapidly excluded. If these differences are small, exclusion will be slow.

![Figure 2: Competitive exclusion and coexistence](image-url)

(A) Differences between species in their competitive ability drive the superior to dominance and the inferior to exclusion. Both rodent species depicted in consume the same size seeds, though the blue species consumes more of them. (B) Niche differences between species hinder competitive exclusion, helping maintain species diversity. The two rodent species depicted in consume different size seeds, an important niche difference, allowing their coexistence.

The central prediction of the competitive exclusion principle, the elimination of all but the best competitor, lies in sharp contrast with what we see in nature; the coexistence of numerous species (Figure 1). This contrast poses an enigma. Ecologists resolve this enigma by reasoning that other species properties must prevent the elimination of the inferior competitors. These are what ecologists call niche differences, species differences that maintain diversity by preventing competitive exclusion (Figure 2b; Chesson 2000, Adler et al. 2007).

The niche is an abstract and often debated concept, but simply put, it defines how a species interacts with its environment (Chase & Leibold 2003). For example, the niches of the two rodent species in Figure 2b include their diet; the quantity and size of seeds consumed. A niche difference between species arises, for example, when one rodent (the blue) tends to consume larger seeds than the other (the orange) (Figure 2b). But how do such niche differences maintain species diversity?

Envision a scenario in which the rodent eating large seeds (the blue) becomes so common that its competitor becomes rare. This shift in rodent abundance will cause a deficit of large seeds and an abundance of small seeds in the habitat. Such a shift will benefit the small seed consuming species (in orange), at the expense of its competitor (in blue). Conversely, if the small seed consuming species becomes common, large seeds would be in abundance, allowing the large seed competitor to recover. Thus, the defining feature of a niche difference is that it causes each species to limit individuals of its own species more than it limits individuals of its competitor (Chesson 2000, Adler et al. 2007). Niche differences thereby distil favorable species that become common and advantage those that are rare, which hinders competitive exclusion and maintains biodiversity (Figure 2b).

With competitive ability differences driving assemblages of species toward dominance by a single competitor, and niche differences opposing competitive exclusion by favoring species that drop to low abundance (Figure 2b), the outcome of competition (exclusion or coexistence) depends on the balance between the two types of species’ differences (Chesson 2000, Adler et al. 2007). If the stabilizing effects of niche differences are stronger than the differences in competitive ability, species will coexist and diversity will be maintained. By contrast, if differences in competitive ability are great, competitive exclusion will occur even with modest niche differences. In our example, this would occur if the rodents differed only slightly in the sizes of seeds consumed, but one species ate far more seeds than the other.

An analogy to the more familiar case of competing businesses reinforces the way ecologists think about species coexistence. Two airlines sharing the same routes are not likely to both stay in business (i.e., coexist) if passengers consistently value one airline over the other (a competitive ability difference). Nevertheless, the less competitive airline can still persist by offering different routes than its superior counterpart, thereby capitalizing on a different customer base (a niche difference). Of course, for coexistence, the offered routes must be sufficiently different, which in ecological language would be expressed as the need for the niche difference to outweigh the difference in competitive ability.

The niche differences studied by ecologists today can be more complex than the example in Figure 2b, but they all share the defining features of our hypothetical example. Figure 3 presents two results from the recent ecological literature. Scientists have shown that coexisting plant species in the arctic use different forms of nitrogen (Figure 3a; Mc Kane & et al. 2002). Such differences can stabilize plant coexistence by disfavoring species that become so abundant that their preferred form of nitrogen becomes less available.
Figure 3: Niche differences ecologists have used innovative field observations and manipulations to quantify niche differences between species

(A) Ecologists studying arctic tundra have used chemical tracers to show that different plant species consume different forms of nitrogen (glycine versus ammonium versus nitrate) (McKane et al. 2002). This forms a niche difference because it causes Carex to compete more with other Carex individuals than it does with Vaccinium. (B) Cherry species limit individuals of their own species more than those of other species via fungal disease. This disease preferentially kills cherry seedlings when near infected parent trees and infected seedlings of their own species (Packer & Clay 2000). Away from trees of their own species (where cherries are at much lower abundance), seedling survival is higher. As shown in the photograph, fungal disease causes seedlings to wilt before dying (Figure 3A redrawn from Nature 415, 68-71; 3B, Nature 404, 278-281). (3B courtesy of Keith Clay)

Other niche differences involve consumers and disease. For example, when species are attacked by a specialist pathogen, a disease that harms only them, individuals are only "contagious" to others of the same species. This causes individuals of the diseased species to limit other individuals of their own species more than they limit their competitors. As is true for resource-based niche differences (Figures 2b and 3a), disease niches can thereby cause species to gain advantages when rare (when disease prevalence is low), and disadvantages when common (when disease prevalence is high). For example, seedlings of Pin Cherry, a North American tree, are more likely to escape fungal disease when rare, and not surrounded by other infected Pin Cherry individuals (Figure 3b; Packer & Clay 2000).

Other important niche differences arise when species grow best different habitats, such as shallow or deep soils for plants, or in different types of years (wet years versus dry years) (Chesson 2000). As long as these and other niche differences sufficiently benefit species that fall to low abundance in their habitat, diversity is maintained.

Although ecologists have a firm handle on the need for niche differences to maintain species diversity, many unresolved questions remain. For example, are there really hundreds of niche differences between species explaining the wide diversity found in tropical forests? Identifying the niche differences operating in specific habitats, and hyper diverse ecological systems (Figure 1) in particular, has proven challenging (Adler et al. 2007, Levine & HilleRisLambers 2009). This is because niche differences can arise through a wide variety of ecological interactions (Figure 3), and may operate over long time scales that are difficult to study. As a consequence, ecologists have yet to determine which niche differences are most important for the maintenance of diversity, and whether the identity of those niches changes with the habitat or organisms studied.

Ecologists also know little about how strongly niche differences stabilize coexistence in natural communities (Levine & HilleRisLambers 2009). Although the competitive exclusion principle states that two species competing for the same resource cannot coexist indefinitely (hence the importance of niches), evenly matched competitors can co-occur for long periods of time without any niche differences. This is the foundation of the recently proposed neutral theory (Hubbell 2001), which suggests that a competitive stalemate might be the best explanation for the diversity of species seen in nature. While ecologists generally agree that species are unlikely to be perfectly matched competitors, the influence of competitive ability differences and niche differences on coexistence remains difficult to quantify in natural habitats (Levine & HilleRisLambers 2009).

How species diversity is maintained may seem an abstract question, of interest only to ecologists. However, the dramatic impacts of humans on the environment, which include increasing global temperatures, the removal of top predators, or the addition of nitrogen (from the use of fertilizers) to habitats, can strongly alter the relative competitive ability and niche differences between co-occurring species. For example, nitrogen deposition can favor weedy species over slow growing competitors by mimicking the importance of competitive ability for nitrogen. The introduction of non-native species into new habitats may allow them to "escape" their natural enemies and become overwhelmingly abundant at the cost of native diversity. A better understanding of the mechanisms that contribute to species diversity will allow ecologists and conservation biologists to better predict and manage future biodiversity.

References and Recommended Reading


Evolution is Change in the Inherited Traits of a Population through Successive Generations

The Hardy-Weinberg Principle

Using Molecular Techniques to Answer Ecological Questions

Mutations Are the Raw Materials of Evolution

Avian Egg Coloration and Visual Ecology

The Ecology of Avian Brood Parasitism

The Geography and Ecology of Diversification in Neotropical Freshwaters

The Maintenance of Species Diversity

Neutral Theory of Species Diversity

Population Genomics

Semelparity and Iteroparity

Why Are Life Histories So Variable?

Comparative Genomics

Case Study: The Glorious, Golden, and Gigantic Quaking Aspen

Cybertaxonomy and Ecology

Molecular Genetic Techniques and Markers for Ecological Research

Resource Partitioning and Why It Matters

Explore This Topic

outline | keywords | Feedback

© 2011 Nature Education

About | Contact | Press Room | Sponsors | Terms of Use | Glossary | Library | Home | Topics | People | Groups | Learning Paths

Natural selection, genetic drift, and gene flow are the mechanisms that cause changes in allele frequencies over time. When one or more of these forces are acting in a population, the population violates the Hardy-Weinberg assumptions, and evolution occurs. The Hardy-Weinberg Theorem thus provides a null model for the study of evolution, and the focus of population genetics is to understand the consequences of violating these assumptions.

In natural populations, the mechanisms of evolution do not act in isolation. This is crucially important to conservation geneticists, who grapple with the implications of these evolutionary processes as they design reserves and model the population dynamics of threatened species in fragmented habitats.

Natural selection occurs when individuals with certain genotypes are more likely than individuals with other genotypes to survive and reproduce, and thus to pass on their alleles to the next generation. As Charles Darwin (1859) argued in On the Origin of Species, if the following conditions are met, natural selection must occur:

1. There is variation among individuals within a population in some trait.
2. This variation is heritable (i.e., there is a genetic basis to the variation, such that offspring tend to resemble their parents in this trait).
3. Variation in this trait is associated with variation in fitness (the average net reproduction of individuals with a given genotype relative to that of individuals with other genotypes).

Directional selection leads to increase over time in the frequency of a favored allele. Consider three genotypes (AA, Aa, and aa) that vary in fitness such that AA individuals produce, on average, more offspring than individuals of the other genotypes. In this case, assuming that the selective regime remains constant and that the action of selection is the only violation of Hardy-Weinberg assumptions, the A allele would become more common each generation and would eventually become fixed in the population. The rate at which an advantageous allele approaches fixation depends in part on the dominance relationships among alleles at the locus in question (Figure 1). The initial increase in frequency of a rare, advantageous, dominant allele is more rapid than that of a rare, advantageous, recessive allele because rare alleles are found mostly in heterozygotes. A new recessive mutation therefore cannot be "seen" by natural selection until it reaches a high enough frequency (perhaps via the random effects of genetic drift — see below) to start appearing in homozygotes. A new dominant mutation, however, is immediately visible to natural selection because its effect on fitness is seen in heterozygotes. Once an advantageous allele has reached a high frequency, deleterious alleles are necessarily rare and thus mostly present in heterozygotes, such that the final approach to fixation is more rapid for an advantageous recessive than for an advantageous dominant allele. As a consequence, natural selection is not as effective as one might naively expect it to be at eliminating deleterious recessive alleles from populations.
Balancing selection, in contrast to directional selection, maintains genetic polymorphism in populations. For example, if heterozygotes at a locus have higher fitness than homozygotes (a scenario known as heterozygote advantage or overdominance), natural selection will maintain multiple alleles at stable equilibrium frequencies. A stable polymorphism can also persist in a population if the fitness associated with a genotype decreases as that genotype increases in frequency (i.e., if there is negative frequency-dependent selection). It is important to note that heterozygote disadvantage (underdominance) and positive frequency-dependent selection can also act at a locus, but neither maintains multiple alleles in a population, and thus neither is a form of balancing selection.

Genetic drift results from the sampling error inherent in the transmission of gametes by individuals in a finite population. The gamete pool of a population in generation $t$ is the total pool of eggs and sperm produced by the individuals in that generation. If the gamete pool were infinite in size, and if there were no selection or mutation acting at a locus with two alleles ($A$ and $a$), we would expect the proportion of gametes containing the $A$ allele to exactly equal the frequency of $A$, and the proportion of gametes containing $a$ to equal the frequency of $a$. Compare this situation to tossing a fair coin. If you were to toss a coin an infinite number of times, the proportion of heads would be 0.50, and the proportion of tails would be 0.50. If you toss a coin only 10 times, however, you shouldn't be too surprised to get 7 heads and 3 tails. This deviation from the expected head and tail frequencies is due to sampling error. The more times you toss the coin, the closer these frequencies should come to 0.50 because sampling error decreases as sample size increases.

In a finite population, the adults in generation $t$ will pass on a finite number of gametes to produce the offspring in generation $t + 1$. The allele frequencies in this gamete pool will generally deviate from the population frequencies in generation $t$ because of sampling error (again, assuming there is no selection at the locus). Allele frequencies will thus change over time in this population due to chance events — that is, the population will undergo genetic drift. The smaller the population size ($N$), the more important the effect of genetic drift. In practice, when modeling the effects of drift, we must consider effective population size ($N_e$), which is essentially the number of breeding individuals, and may differ from the census size, $N$, under various scenarios, including unequal sex ratio, certain mating structures, and temporal fluctuations in population size.

At a locus with multiple neutral alleles (alleles that are identical in their effects on fitness), genetic drift leads to fixation of one of the alleles in a population and thus to the loss of other alleles, such that heterozygosity in the population decays to zero. At any given time, the probability that one of these neutral alleles will eventually be fixed equals that allele's frequency in the population. We can think about this issue in terms of multiple replicate populations, each of which represents a deme (subpopulation) within a metapopulation (collection of demes). Given 10 finite demes of equal $N_e$, each with a starting frequency of the $A$ allele of 0.5, we would expect eventual fixation of $A$ in 5 demes, and eventual loss of $A$ in 5 demes. Our observations are likely to deviate from these expectations to some extent because we are considering a finite number of demes (Figure 2). Genetic drift thus removes genetic variation within demes but leads to differentiation among demes, completely through random changes in allele frequencies.
Gene flow is the movement of genes into or out of a population. Such movement may be due to migration of individual organisms that reproduce in their new populations, or to the movement of gametes (e.g., as a consequence of pollen transfer among plants). In the absence of natural selection and genetic drift, gene flow leads to genetic homogeneity among demes within a metapopulation, such that, for a given locus, allele frequencies will reach equilibrium values equal to the average frequencies across the metapopulation. In contrast, restricted gene flow promotes population divergence via selection and drift, which, if persistent, can lead to speciation.

Natural selection, genetic drift and gene flow do not act in isolation, so we must consider how the interplay among these mechanisms influences evolutionary trajectories in natural populations. This issue is crucially important to conservation geneticists, who grapple with the implications of these evolutionary processes as they design reserves and model the population dynamics of threatened species in fragmented habitats. All real populations are finite, and thus subject to the effects of genetic drift. In an infinite population, we expect directional selection to eventually fix an advantageous allele, but this will not necessarily happen in a finite population, because the effects of drift can overcome the effects of selection if selection is weak and/or the population is small. Loss of genetic variation due to drift is of particular concern in small, threatened populations, in which fixation of deleterious alleles can reduce population viability and raise the risk of extinction. Even if conservation efforts boost population growth, low heterozygosity is likely to persist, since bottlenecks (periods of reduced population size) have a more pronounced influence on Ne than periods of larger population size.

We have already seen that genetic drift leads to differentiation among demes within a metapopulation. If we assume a simple model in which individuals have equal probabilities of dispersing among all demes (each of effective size Ne), within a metapopulation, then the migration rate (m) is the fraction of gene copies within a deme introduced via immigration per generation. According to a commonly used approximation, the introduction of only one migrant per generation (Nm = 1) constitutes sufficient gene flow to counteract the diversifying effects of genetic drift in a metapopulation.

Natural selection can produce genetic variation among demes within a metapopulation if different selective pressures prevail in different demes. If Ne is large enough to discount the effects of genetic drift, then we expect directional selection to fix the favored allele within a given focal deme. However, the continual introduction, via gene flow, of alleles that are advantageous in other demes but deleterious in the focal deme, can counteract the effects of selection. In this scenario, the deleterious allele will remain at an intermediate equilibrium frequency that reflects the balance between gene flow and natural selection.

Conclusion
The common conception of evolution focuses on change due to natural selection. Natural selection is certainly an important mechanism of allele-frequency change, and it is the only mechanism that generates adaptation of organisms to their environments. Other mechanisms, however, can also change allele frequencies, often in ways that oppose the influence of selection. A nuanced understanding of evolution demands that we consider such mechanisms as genetic drift and gene flow, and that we recognize the error in assuming that selection will always drive populations toward the most well adapted state.

References and Recommended Reading

Explore This Topic

<table>
<thead>
<tr>
<th>BASIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evolution Is Change in the Inherited Traits of a Population through Successive Generations</td>
</tr>
<tr>
<td>The Hardy-Weinberg Principle</td>
</tr>
<tr>
<td>Using Molecular Techniques to Answer Ecological Questions</td>
</tr>
<tr>
<td>Mutations Are the Raw Materials of Evolution</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>INTERMEDIATE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Why Are Life Histories So Variable?</td>
</tr>
<tr>
<td>Comparative Genomics</td>
</tr>
<tr>
<td>Case Study: The Glorious, Golden, and Gigantic Quaking Aspen</td>
</tr>
<tr>
<td>Cybertaxonomy and Ecology</td>
</tr>
<tr>
<td>Molecular Genetic Techniques and Markers for Ecological Research</td>
</tr>
<tr>
<td>Resource Partitioning and Why It Matters</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ADVANCED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avian Egg Coloration and Visual Ecology</td>
</tr>
<tr>
<td>The Ecology of Avian Brood Parasitism</td>
</tr>
<tr>
<td>The Geography and Ecology of Diversification in Neotropical Freshwaters</td>
</tr>
<tr>
<td>The Maintenance of Species Diversity</td>
</tr>
<tr>
<td>Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations</td>
</tr>
<tr>
<td>Neutral Theory of Species Diversity</td>
</tr>
<tr>
<td>Population Genomics</td>
</tr>
<tr>
<td>Semelparity and Iteroparity</td>
</tr>
</tbody>
</table>
Neutral Theory of Species Diversity

By: W. Stanley Harpole (Department of Ecology, Evolution, and Organismal Biology, Iowa State University) © 2010 Nature Education


No need for niches? Neutral theory explains biodiversity when species are identical.

Niche differences, or the unique ways that each species “makes its living” in nature, are the classical explanation that ecologists have used since Darwin to explain the amazing diversity of life on Earth. More precisely, a species’ niche encompasses all of the factors it requires for growth and reproduction and how a species impacts its environment. For example, plants require water and nutrients at some minimum amounts, and by growing, plants decrease the availability of those resources, which negatively affects the growth of competitors. Because many factors limit organisms, and because no organism is best adapted for all conditions, species have tradeoffs, which allow them to perform better in some environments, but necessarily worse in others. Niche differences are a mechanism that can maintain biodiversity by allowing species to coexist. Building on foundational ideas described in island biogeography and the neutral theory of molecular evolution, the neutral theory of species diversity makes the provocative assumption that all individuals are ecologically identical, and that niche differences are not needed to explain biodiversity patterns. Individuals of certain species may all share characteristics that make them look or function different from other species, but those differences do not influence diversity. An individual in a community interacts with and experiences its neighbors as though they were exactly the same, regardless of species. This assumption of equivalence is the essential feature of neutrality, which differs from typical niche-based assumptions that an individual’s fitness depends on who its neighbors are: are they stronger or weaker competitors or do they belong to different species with different niche requirements?

Building on foundational ideas described in island biogeography and the neutral theory of molecular evolution, the neutral theory of species diversity makes the provocative assumption that all individuals are ecologically identical, and that niche differences are not needed to explain biodiversity patterns. Individuals of certain species may all share characteristics that make them look or function different from other species, but those differences do not influence diversity. An individual in a community interacts with and experiences its neighbors as though they were exactly the same, regardless of species. This assumption of equivalence is the essential feature of neutrality, which differs from typical niche-based assumptions that an individual’s fitness depends on who its neighbors are: are they stronger or weaker competitors or do they belong to different species with different niche requirements?

Figure 1: Neutral and niche differences

(A) Very similar herbivores might be considered to be equivalent and essentially neutral. (B) Herbivores that eat different plants, or even the same plants but at different times or at different heights, would have different or overlapping niches. In contrast, neutral theory suggests that even species that look very different from each other might be considered to be ecologically equivalent. (C-E) Species with greatest fitness at some point along an environmental gradient or niche axis. Neutral species have completely overlapping niches; they share the same niche and their fitness changes identically along an environmental gradient or niche axis. Greater niche differences correspond to less niche overlap between species; species differ in their fitness at different points along an environmental gradient or niche axis.

How Neutral Theory Works

Under the neutral theory, highly diverse communities of equivalent species arise because chance extinctions are balanced by speciation. Specifically, the assumption of fitness equivalence combined with stochastic or random processes that include death, immigration from a regional pool of species, and speciation can lead to species-rich communities (Figure 2). As an example, imagine a field, which will be the local community, made up of many species of plants. Plants in the surroundings will represent the regional species pool. The field is thus part of a larger collection of plant communities called a meta-community. Individuals in the local community die at random and create openings for seeds to grow. Individuals from the meta-community, and from the local community, randomly disperse their seeds into the field (Figure 2). If there are more individuals of some species than others they will contribute more seeds than will rare species, but each individual seed has an equal chance of establishing. Individuals are in that sense
Competing for open sites. If dispersal from the meta-community is strong, the local community will look like a small version of the region; if dispersal from outside is weak, random deaths and extinctions combined with random mutations and speciation will cause the local community to drift and differ more and more from other communities over time, but in an unpredictable way. This random change in species abundance over time is termed ecological drift. There can be a limit to the number of individuals in the local community — this is known as a zero sum assumption: if the community is full, a new individual can only establish if another one dies and makes space (Figure 2).

Figure 2: Modeling a neutral process
A local community (a) represents a subset of all of the species found in the region or meta-community. Some individuals die at random in a local community (16 identical individuals from 6 species, in this example), which creates open sites (b). Open sites are then filled by random dispersal from both the meta-community and from the local community (c), including the addition of a new species from the meta-community. Random mutation (not shown) can also lead to the formation of new species. The sequence repeats leading to ecological drift where species abundances change randomly over time.

What Neutral Theory Is; What It Isn’t
Random death, dispersal and speciation are all important features of the neutral theory of biodiversity, but its one key, essential feature is the assumption of identical individuals (species may have differences, but those differences do not matter because all individuals have the same fitness and experience each other identically). The other features are assumptions about the processes that determine community assembly, or how species are added to and lost from communities, and how communities change over time — their dynamics. Another aspect of neutral theory is that it only applies to groups of similarly functioning species: trees in a forest or corals in a reef, and not to species of different size or trophic position, like microbes and elephants, or plants and herbivores. Also, there is no single neutral theory model, and different neutral models make different assumptions about these other processes. For example, one could imagine a neutral community — made up of identical individuals of multiple species — without immigration. Neutral models don’t need to follow the zero sum assumption: a local community could remain partly empty, or alternatively the numbers of individuals might be allowed increase in a model continuously. Stochastic processes are important in neutral models for communities to change over time, but some parameters might be random while others might be non-random: annual plants always die at the end of the year. Niche models, where individuals of different species do differ from each other and those differences matter for their fitness, can also be stochastic, and some purely deterministic or truly non-random processes can also be unpredictable (see chaos theory) and only apparently random. Stochasticity or randomness is often just a simplification we make when we can’t predict exactly the outcome of an event: assuming something is random allows us to conveniently describe a process in terms of probability or chance.

Although dispersal, stochasticity and speciation are not unique to the neutral theory, neutral models are more interesting and useful when we add in things like dispersal and stochasticity. For this reason, neutral theory is often described as a “dispersal-assemble” theory or a “stochastic” theory, even though neither dispersal nor stochasticity is a feature uniquely or necessarily neutral. Dispersal and reproductive traits are in fact another way that species can differ in their fitness, and how organisms move through space can be an important component of a species’ niche. Consider the enormous variety shown by flowering plants in their fruits (coconuts to dandelion seeds) and the diverse ways plants can disperse by wind, water or animals, as well as their different mating strategies, germination and pollination mechanisms. Dispersal may often be highly unpredictable, but it is not necessarily neutral.

Dispersal and speciation processes in neutral models can lead to highly diverse communities. But the coexistence of species in neutral communities is unstable — there are no mechanisms that cause one species to remain dominant or prevent rare species from going extinct. Because neutral processes are driven by random events, and because all individuals are competitively identical, their abundances either increase or decrease purely by chance. In a closed system, stable coexistence, or long-term persisting species, can only occur when there are niche differences that cause individuals to compete most strongly with individuals of their own species compared to those of other species. Niche-based stabilizing mechanisms limit the growth of species when they become very abundant, while at the same time stabilizing mechanisms allow rare species to increase because they enjoy higher fitness when surrounded by neighbors of different species with whom they compete less strongly.

Pattern versus Process
Neutral models can predict realistic species diversity patterns from just a few parameters. One parameter is the Fundamental Biodiversity Number, which is larger with greater numbers of individuals in the meta-community and with greater speciation rates. With the fundamental biodiversity number and estimates of dispersal, neutral models can predict the number of species and their relative abundance patterns in different systems. For example, when we plot the rank of a species against its abundance in a community, we usually find just a few super-abundant species (high rank) along with many very rare species (low rank) (Figure 3). These species abundance distributions are one type of pattern that neutral models have been very good at predicting. But it turns out that many types of alternative niche models do so just as well, which makes these pattern-matching approaches a fairly
weak test: showing a pattern doesn't necessarily tell you the process responsible. Where neutral models have consistently failed is in stronger tests, such as predicting which species or traits of species should be abundant, or under what environmental conditions some species increase while others decrease.

Figure 3: Species abundance patterns

(A) The individuals from the example in Figure 2c are ranked 1 through 7, from most to least abundant species. (B) An example of a simulated community of 100 species showing a characteristic pattern of species rank abundance.

The Utility of Neutral Theory

Neutral theory is still a powerful and useful concept for several reasons. Stephen Hubbell’s 2001 monograph, The Unified Neutral Theory of Biodiversity and Biogeography, has sparked vigorous debate among ecologists, and has led to more rigorous, and much needed, tests of niche mechanisms and explanations of biodiversity. Ironically, neutral theory has reinvigorated niche theory. As with all models, the neutral model is a simplification, albeit a drastic one, of processes we think important in the natural world (e.g., competition, dispersal). Thus, the strength of the neutral model is that it provides us with a logical place to start: an elegant and simple null model, with clear and testable assumptions and predictions. We can then ask if other mechanisms, and their added complexity, are necessary to explain what we observe.

Summary

The neutral theory of species diversity starts with the key assumption that all individuals in a community of trophically similar species are ecologically identical. Neutral models that additionally include random death, speciation, extinction, and dispersal from the meta-community can lead to highly diverse communities that have similar species abundance patterns to what we observe in real communities. The abundances of species in neutral models fluctuate randomly over time leading to ecological drift, where diversity is due to unstable coexistence and the balance between extinction and speciation, in contrast to niche models that assume the importance of species’ niche differences and stabilizing mechanisms. Neutral theory provides a null model, or a starting point, from which we can test niche-based hypotheses for how species’ evolutionary adaptations and niches maintain biodiversity.

References and Recommended Reading


Explore This Topic

**BASIC**
- Evolution Is Change in the Inherited Traits of a Population through Successive Generations
- The Hardy-Weinberg Principle
- Using Molecular Techniques to Answer Ecological Questions
- Mutations Are the Raw Materials of Evolution

**ADVANCED**
- Avian Egg Coloration and Visual Ecology
- The Ecology of Avian Brood Parasitism
- The Geography and Ecology of Diversification in Neotropical Freshwaters
- The Maintenance of Species Diversity
- Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations
- Neutral Theory of Species Diversity
- Population Genomics

**INTERMEDIATE**
- Why Are Life Histories So Variable?
- Comparative Genomics
- Case Study: The Glorious, Golden, and Gigantic Quaking Aspen
- Cybertaxonomy and Ecology
- Molecular Genetic Techniques and Markers for Ecological Research
- Resource Partitioning and Why It Matters
Population Genomics

By: Patrick Nosil (EBIO, University of Colorado at Boulder) & Alex Buerkle (Department of Botany, University of Wyoming) © 2010 Nature Education

How do evolutionary processes affect the genome? The field of population genomics surveys patterns in the genome within and among populations to make inferences about evolution and the genome.

Variation in Population Divergence Among Genomic Regions

Independent evolution of populations leads to their genetic divergence. Different regions of the genome are expected to exhibit highly variable levels of genetic divergence (reviewed by Nosil et al. 2009), ranging from genomic regions exhibiting little to no differentiation between populations to regions where genetic divergence is extremely pronounced (Figure 1). This pattern of variation in population divergence across regions of the genome has been referred to as heterogeneous genomic divergence (Nosil et al. 2009). Genomic divergence is expected to be highly heterogeneous during the process of population divergence and species formation, during which genetic differentiation associated with divergent natural selection accumulates in some regions while the homogenizing effects of gene flow or inadequate time for random differentiation by genetic drift preclude divergence in other regions. Many factors contribute to heterogeneous genomic divergence, including selection arising from ecological causes or genetic conflict, the stochastic effects of genetic drift, variable mutation rates, the genetic basis of traits under selection, and genetic linkage among genes on chromosomes. The patterns of genomic differentiation among populations record and integrate across these different historical evolutionary and genetic processes, thereby offering biologists opportunities to reconstruct the forces that shaped evolutionary divergence.

Figure 1: Three arbitrary classes of loci embedded within a continuous distribution of $F_{ST}$ values

(a) Selected loci, or those very tightly linked to them, exhibit particularly high $F_{ST}$ and thus are recognized as unlikely, statistical outliers. (b) Neutral loci that are weakly-linked to selected loci exhibit $F_{ST}$ values that are somewhat elevated, but insufficiently so to be designated outlier loci. (c) Neutral unlinked loci exhibit low $F_{ST}$.

© 2010 Nature Education Modified from Egan et al. (2008) and reprinted with permission of Wiley-Blackwell. All rights reserved.

We focus here on the contributions of divergent natural selection to population divergence. Such divergent selection will pull apart allele frequencies between populations at loci under selection and those physically-linked to them, resulting in strong differentiation of regions affected by selection. This might occur even if the remainder of the genome remains relatively undifferentiated. Thus, loci under divergent selection and those tightly physically-linked to them should exhibit greater differentiation than weakly-linked or unlinked neutral regions. If only a subset of loci experiences divergent selection, the selected loci can be recognized as exceptional relative to the remainder of the genome and as outlier loci whose genetic divergence exceeds neutral expectations (Figure 2).
The field of population genomics examines patterns in the genome, often using genome scans that examine genetic divergence between populations at numerous loci across the genome. The degree of genetic divergence is often measured using fixation indices such as FST, with larger index values representing greater differentiation between populations.

A Brief History of Population Genomics

Population genomic analyses require multi-locus data sets from multiple populations and identify non-neutral or outlier loci by contrasting patterns of population divergence among genetic regions. This approach was first proposed by Lewontin & Krakauer (1973), and numerous variations on this original method now exist (Beaumont 2005, Foll & Gaggiotti 2008, Gompert et al. [in review]). Perhaps the most commonly employed of these methods, particularly in non-model organisms, is the FST outlier analysis developed by Beaumont & Nichols (1996). This test contrasts FST for individual loci with an expected null distribution of FST based on a neutral model. Under this approach, loci with very high levels of differentiation between populations (i.e., high FST) are considered candidates for positive or divergent selection whereas loci with exceptionally low FST are regarded as candidates for balancing selection. However, many FST outlier analyses may be biased by departures from the assumed demographic history (Excoffier et al. 2009). An alternative approach to obtain a null distribution of population genetic differentiation is to assume that FST for individual loci represent independent draws from a common, underlying distribution that characterizes the neutral divergence across the genome and can be estimated directly from multi-locus data (Foll & Gaggiotti 2008; Figure 3). This alternative approach is more robust to different demographic histories. Recent advances in computational methods and molecular biology (including next-generation sequencing) allow patterns of genomic divergence to be investigated at previously unattainable scales. We now turn to describing in some more detail three case studies of population genomic analyses.

Figure 3: Statistics of population differentiation can be estimated by Bayesian methods, which provide a probabilistic framework in which to interpret differentiation of individual loci. Differentiation among populations of Lycaeides butterflies in North America was estimated (Gompert et al. 2010) and summarized in a genome-level estimate of ΦST (a) and its average deviation (b). This analysis illustrated the high variation among loci across the genome (c, arbitrary set of 200 scored loci), some of which is likely to have been shaped by divergent natural selection.

© 2010 Nature Education All rights reserved.
Case Studies

Population Genomic Evidence for Recent and Rapid Evolutionary Adaptation in Humans

As humans expanded into new geographic regions and came to occupy novel environments, our ancestors experienced diverse patterns of natural selection that were recorded in the genomes of divergent populations. For example, humans moved from low elevations to occupy some of the highest plateaus and mountain ranges in the world, including the plateaus of Central Asia and the Andes of South America. These populations exhibit heritable physiological attributes that allow individuals to function at high altitudes (3250–4500 m) with low oxygen concentrations that are challenging to humans from lower elevations. Interestingly, humans from the Tibetan plateau exhibit several physiological attributes that differ from those of Andean highlanders, suggesting that independent evolutionary trajectories led to different adaptations to high altitude. Three studies have used genome scans to identify genes with exceptional allele frequency shifts between populations that were likely targets of divergent natural selection in Tibetan highlanders relative to other human populations (reviewed in Storz 2010). Several genes were identified as associated with a history of positive selection in Tibetan highlanders; the gene EPAS1 was identified as one of the most exceptional genes in each study and was also shown to be associated with presumably adaptive variation in hemoglobin concentration.

A second example of adaptive divergence among human populations is related to the persistence of lactase production in adults. Lactase production in the gut functions in the digestion of the milk sugar lactose, and lactase production in adults is prevalent in humans with ancestry in northern and western Europe and pastoralist populations in several regions of the world. Adult persistence of lactase is much less common in southern Europe and the Middle East and rare in non-pastoralist populations in Asia and Africa. Genetic studies have associated adult persistence of lactase with different genes in different populations that exhibit the trait at high frequency, indicating that the trait has arisen independently in multiple populations (Tishkoff et al. 2007). Remarkably, genomic variation surrounding each of the underlying genes is consistent with strong natural selection within the last several thousand years increasing the frequency of the derived, adaptive alleles (Tishkoff et al. 2007).

Genomic Islands in Anopheles Mosquitoes

To help understand regions of divergence in the genome, evolutionary biologists have developed the concept of "genomic islands of divergence" (Turner et al. 2005; Figure 4). A genomic island is any gene region, be it a single nucleotide or an entire chromosome, that exhibits significantly greater differentiation than expected under neutrality (and thus generally greater divergence than observed in neighboring genomic regions). The metaphor, therefore, draws a parallel between genetic differentiation observed along a chromosome and the topography of oceanic islands and the contiguous sea floor to which they are connected. Following this metaphor, sea level represents the threshold above which observed differentiation is significantly greater than expected by neutral evolution alone. Thus, an island is composed of both directly selected and tightly linked (potentially neutral) loci.

![Figure 4: An empirical example of genomic islands of divergence involving incipient species of Anopheles gambiae](image)

Figure 4 depicts an empirical example of a genomic island from population genomic studies of different forms of Anopheles gambiae mosquitoes. These insects are vectors for malaria, and Turner et al. (2005) surveyed divergence across the genome of the different mosquito forms. They found just a few regions that were differentiated (i.e., a few isolated genomic islands) between the forms. In a follow-up study, Turner & Hahn (2007) sequenced portions of all annotated genes within the smaller island were sequenced. © 2010 Nature Education Modified from the original studies and reprinted with permission of the Public Library of Science and the Society of Molecular Biology and Evolution. All rights reserved.

Other Applications of Population Genomics

In addition to genome scans for differentiation, population genomics also includes many other diverse analyses of population genomic variation. These include research that more directly ties or genetically maps variation in phenotypes (e.g., body size, bill length, feather color, mating behavior) to genetic variation in various organisms. Similarly, researchers use other signatures of natural selection (e.g., extended haplotype blocks) to detect genomic regions that are likely to have experienced selection. As technology has allowed the rate of genomic data acquisition to increase enormously, an increasing range of biological questions can now be addressed at the scale of the genome rather than focusing on very small fractions of genomic variance.
Caveats
Genome scans of differentiation, by virtue of detecting divergent selection via looking for the most differentiated regions, are inevitably destined to underestimate how widespread the effects of selection are in the genome. In other words, genome scans will often fail to identify regions that are affected by divergent selection but only weakly so. A recent analysis of divergent selection in two host forms of Rhagoletis flies exemplifies this issue (Michel et al. 2010). This study reported that standard outlier analyses detected evidence for selection on only a few exceptionally differentiated genomic regions. In contrast, results from an experiment where the fly’s genome was directly subjected to divergent selection revealed that selection was affecting much of the genome, albeit often quite weakly. The prevalence of selection may also be underestimated because most analytical methods are unlikely to detect soft sweeps involving smaller shifts in the allele frequency spectrum of multiple loci and are dependent on the genetic architecture of adaptation.

Conclusions and Future Directions
Population genomics holds great promise for understanding the evolutionary processes affecting genomes. However, population genomics is not a panacea, and analyses must increasingly be conducted with care. For example, the stochastic nature of next-generation sequencing technologies creates uneven coverage among individuals and genetic regions, which misses data for many individuals and loci, and thus increased uncertainty in the genotypes of individuals relative to traditional Sanger sequencing. Appropriately modeling and accounting for this uncertainty is important and preferable to discarding large amounts of sequence data (Gompert et al. 2010). Further advances in molecular and computational biology and increased computing power itself will allow more powerful and accurate application of population genomics.

References and Recommended Reading
Foll, M. & Gaggiotti, O. A genome scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics 185, 977–993 (2008).
Gompert Z. & Buerkle C. A. Analytical tools for next-generation sequence data. In review.
Semelparity and Iteroparity

Why do some organisms die immediately after reproducing (some salmon and bamboos, many insects, and all grain crops), while others live on to reproduce repeatedly (most plants and vertebrates)?

Semelparity

Many plant and animal species have life histories characterized by death after first reproduction. This is called semelparity, and its alternative (living to reproduce repeatedly) is called iteroparity. In plants, the terms monocarpy and polycarpy are sometimes used instead of semelparity and iteroparity. However, monocarpy can also be used more restrictively to describe plants in which individual shoots die after reproducing, but not necessarily the entire plant.

Examples of short-lived semelparous species include annual and biennial plants (including all grain crops, and many herbaceous vegetables), and certain invertebrate species, including many spiders (Figure 1). There are even a few semelparous marsupial mammals in Australia. It is important to note that while all annual plants are semelparous, not all perennial plants are iteroparous. There are a wide variety of plant and animal species that live for many years before a single, massive, fatal reproductive episode (certain species of salmon, bamboo, and century plants, Figure 2).

Semelparity has evolved independently many times, apparently as a derived state from iteroparous ancestors. This dramatic life history difference offers a model system for theoretical and empirical studies of adaptive evolution.

Dilemma and Cost of Reproduction

Natural selection maximizes total lifetime reproductive output. So how could evolution ever favor programmed death after first reproduction? A key clue lies in the observation that semelparous species typically produce more offspring in their single reproductive episode than closely related species do in any one of theirs. It appears that when an organism does not need to withhold some resources to ensure future survival and reproduction, it can mobilize virtually all available resources to put into a single, massive reproductive episode. For example, this fecundity advantage is two to fivefold in plants. So the essential question becomes, "Under what conditions does the increase in fecundity associated with semelparity more than compensate for the loss of potential subsequent reproductive episodes?"
Theoretical Approaches
This question has been the subject of a rich theoretical literature. These models fall into three classes, all of which assume a tradeoff between reproduction and survival:

1. **Demographic models** predict that when adult survival is low enough (relative to juvenile survival), evolution should abandon withholding resources for a future reproduction that is unlikely, and instead favor semelparity (Figure 3).

2. **Bet-hedging models** predict that when adult survival is highly variable, evolution should favor iteroparity, because it does not risk putting all reproductive effort into a single reproductive episode.

3. **Models incorporating non-linear patterns of reproductive costs and benefits** predict that semelparity should be more likely to evolve when most of the costs of reproduction (reduction in future survival or reproduction caused by increases in current reproduction) happen even at low levels of reproductive effort, or conversely, when the benefits of reproduction accrue most rapidly at high levels of reproductive effort.
Empirical Evidence

Despite the abundance of theoretical models for the evolution of semelparity, direct empirical tests for each remain limited. For example, many species of annual plants are desert species or weedy species that are early arrivals after disturbance in many ecosystems. Both of these groups are subject to high variation in survivorship, in opposition to the predictions of the bet-hedging model. In a particularly elegant test of the non-linearity model, it was demonstrated that the taller inflorescences of semelparous yucca species produced disproportionately more seeds than smaller inflorescences, but that this was not true in iteroparous yucca species. Similarly, pollinators preferred taller inflorescences of semelparous yucca species, but not iteroparous species. Although this observation fits the non-linear theory nicely, it has been pointed out that many of these species may not be pollinator-limited, and that inflorescence height patterns may be physiological consequences of life history differences, and not their evolutionary causes.

There have been several more successful tests of the demographic model, and they all show that semelparity is more likely in species (or populations) where adult survival would be low even if they were not semelparous. These tests come from diverse systems, including spiders, fish, an alpine mustard, and a giant rosette plant. In addition, both desert annuals and early successional annuals live in habitats where survival beyond the growing season might be expected to be low.

Synchronous Semelparity

There is an unusual pattern in semelparous plants characterized by single-aged populations that live for many years, then synchronously flower and die. Certain bamboos species are well known to exhibit this pattern, but other examples include certain palm species, shrubs in the family Acanthaceae, and even a tropical forest canopy tree. All of these grow in mesic forests that are climatically more moderate than the extreme environments characteristic of most semelparous species (e.g., deserts, alpine habitats, bogs, disturbed sites). Periodic cicadas in the eastern U.S. also exhibit this pattern. Predator satiation has been invoked to explain both synchrony and semelparity in these species, but there is no widespread consensus on its causes.

Species "Approaching" Semelparity

Semelparity and iteroparity have been represented here as a simple dichotomy. Nevertheless, the conceptual framework can be applied more generally. Several examples have been documented where high levels of adult mortality appear to be related to iteroparous life histories characterized by early reproduction that is more frequent and/or more intense. These include subalpine fir trees, patas monkeys, and several insect species.

Semelparity in Grain Crops

It is probably no coincidence that many herbaceous crops, including virtually all grain crops, are annuals. Their semelparity results in far higher yields than if they were iteroparous. It is likely that when selecting grain species for cultivation, early farmers deliberately chose those species with the highest yields, which were annuals, or selected strongly enough for high yields that iteroparous species evolved into semelparous species. The closest relatives of both rice and maize are iteroparous.

Given our dependence on semelparous species, it is important that we better understand the evolution and physiology of this curious life history.

References and Recommended Reading


Evolution Is Change in the Inherited Traits of a Population through Successive Generations

The Hardy-Weinberg Principle

Using Molecular Techniques to Answer Ecological Questions

Mutations Are the Raw Materials of Evolution

Avian Egg Coloration and Visual Ecology

The Ecology of Avian Brood Parasitism

The Geography and Ecology of Diversification in Neotropical Freshwaters

The Maintenance of Species Diversity

Natural Selection, Genetic Drift, and Gene Flow Do Not Act in Isolation in Natural Populations

Neutral Theory of Species Diversity

Population Genomics

Semelparity and Iteroparity