

## EVOLUTION

# Watching speciation in action

An interplay between environmental and genetic change is responsible for the emergence of new species

By **B. Rosemary Grant** and **Peter R. Grant**

Charles Darwin closed his first edition of *On the Origin of Species* with the poetic words: “There is grandeur in this view of life, ... whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved” (1). Today, scientists are using genetics to understand how species multiply, and ecological and behavioral knowledge to understand why they do so. However, many questions remain about the sources of genetic variation and how new phenotypes arise in response to environmental change. Recent research has revealed unexpected origins of genetic variation, providing crucial insights into phenotypic divergence and the evolutionary effects of rare events triggered by global climatic change.

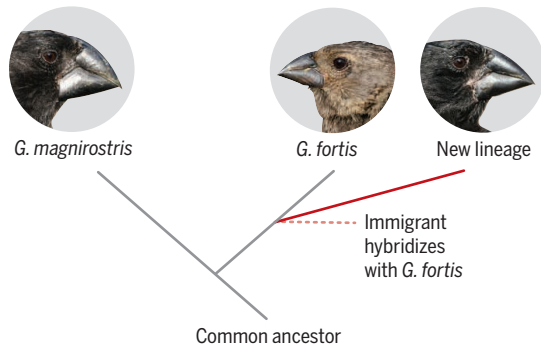
Young adaptive radiations are especially suitable for exploring the causes of speciation. Such radiations are groups of species that have diversified relatively recently and rapidly from a common ancestor and that are probably still diverging. The hundreds of species of cichlid fish in the Great Lakes of Africa are the most celebrated example of rampant and rapid speciation (2). By comparison, Darwin’s finches in the Galápagos archipelago are less spectacular, with fewer than two dozen species having originated in the past 1 million to 2 million years. But for investigating changes in fitness through time, they—unlike cichlids—have the advantage that survival and breeding success of marked individuals can be directly documented by observation. In a 40-year study of four species of finches on the small, uninhabited island of Daphne Major, we have shown that when severe droughts occur and many finches die of starvation, survival depends on the particular types of food available, beak size and shape, and the presence or absence of competitor species (3). A small net shift in

body size, beak size, and beak shape is a small step toward the formation of a new finch species.

Species diverge morphologically and ecologically when competing for limited food resources. As they diverge, the likelihood of interbreeding declines. But what are the genetic pathways underpinning these changes? In Darwin’s finches, five genes coding for signaling molecules (*BMP4*, *CAM*, *TGFβIIr*, *β-catenin*, and *Dickkopf-3*) affect beak size and shape and have different expression patterns in different species [summarized in (3)]. The regulation of these molecules must have changed as species

## One route to speciation

Field observations have shown how an immigrant finch hybridized with the medium ground finch (*Geospiza fortis*) on Daphne Major in the Galápagos archipelago. The resulting new endogamous lineage differs in size and song from the other resident species on the island.



diverged morphologically. In addition, two transcription factor genes (*HMG2* and *ALX1*) are associated with beak characteristics. These transcription factors vary among species but also within populations, allowing the tracking of alleles through selection events. For example, we have found that a striking shift in *HMG2* allele frequency in the medium ground finch (*Geospiza fortis*) population occurred in association with selection on beak size during a drought (4).

Genomic studies can thus identify the genetic basis of ecologically important phenotypes. However, without intensive field study of song, mating patterns, feeding behavior, diets, survival, and environmental fluctuations, we would not know the causes and fitness consequences of selection. Nor would we know that a single immigrant

finch was responsible for the emergence of a new lineage on Daphne Major (3). This bird hybridized with a resident species, and after two generations of gene exchange, the descendants, of mixed ancestry and genetic composition, bred only with each other, thereby forming a population that is reproductively isolated from the other species (see the figure).

In ecological field studies of other species, genetic variation is generally less well known than is the role of selection on phenotypes, although this is changing rapidly because of the increasing availability of genetic tools. The following examples demonstrate the importance of ecological and behavioral knowledge for interpreting genetic data. They also illustrate the diverse ways in which genetic variation is generated and underlies selectable phenotypic variation. These include transposable elements, mutations and inversions, standing variation, introgressive hybridization, and release of cryptic variation.

A well-known example of selection on two discrete forms of a species is the peppered moth (*Biston betularia*) in England. A dark-colored form was first seen in Manchester in 1848, and the rise and fall of its frequency has been well documented as a case of camouflage to hide from avian predators on soot-covered backgrounds. In a recent cloning and sequencing study (5), van’t Hof *et al.* showed that a transposon is the cause of the black morph. This discovery, combined with recent research on cichlid fish genomes (2), suggests that transposable elements may play a more important role in generating variation among species in ecologically important morphological traits than is currently realized.

Other field-based studies illustrate the role of mutation and inversions. For example, Rausher and Delph have shown that in flowering plants of the genera *Ipomoea* and *Penstemon*, transitions in color are often asymmetric, because they involve loss-of-function mutations in the anthocyanin biosynthesis pathway loci that constrain reversals (6). A transition from blue (bee-pollinated) to red (hummingbird-pollinated) is significantly more frequent than the reverse. Another phenotypic puzzle that has recently been solved concerns the ruff (*Philomachus pugnax*), a wading bird with an unusual mating system in which three male forms, differing in plumage and behavior, compete for females on a courting arena (lek). Lamichhaney *et al.* have shown that the different forms are controlled by a large inversion that arose about 3.8 million years ago and subsequently accumulated

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Genetic variation in eye size is exposed when surface varieties of *Astyanax mexicanus* are raised in caves.



genetic mutations (7). In a third field study, Linnen *et al.* investigated the light coat color in a Nebraska population of sand hill deer mice (*Peromyscus maniculatus*). They found that changes in coat color were the result of selection on not one but multiple mutations in the *Agouti* locus (8).

In closely related species that have recently diverged, selection is expected to occur mainly on preexisting variation. At the end of the last ice age, marine three-spined sticklebacks (*Gasterosteus aculeatus*) in western North America repeatedly invaded freshwater habitats, became isolated, and diverged through similar genetic mechanisms into forms that live in surface waters and others that live in bottom waters (9). For example, loss of the pelvic apparatus is controlled by the transcription factor *Pitx1*, and armor plating by the signaling protein ectodysplasin A. This phenomenon, repeated use of the same genetic pathway, has also been found in hemoglobin adaptation of birds to low oxygen levels at high altitudes. Here, as may be the case generally, closely related species use similar genes, whereas more distantly related species use different genetic pathways that depend on their genetic backgrounds (10).

Some of those different genes come from other species. Introgressive hybridization—that is, gene exchange between species as a result of hybrids backcrossing to a parental species—is a powerful means of increasing standing genetic and phenotypic variation. It introduces alleles that contribute to adaptation to an altered environment, as found in the Darwin's finch study (4). Examples include the genes involved in Mullerian mimicry in *Heliconius* butterflies (11) and

those governing longevity and insecticide resistance in *Anopheles* mosquitoes (12). Likewise, genes that confer resistance to the rodenticide warfarin have been transmitted between populations of the African mouse *Mus spretus* and the European *M. musculus* (13). Even more remarkable, and similar to introgressive hybridization, is the passage of genes from bacteria and fungi into eukaryote genomes through horizontal gene transfer. An example is the Asian longhorn beetle *Anoplophora glabripennis*, an invasive pest of various tree species. The beetles acquired genes encoding enzymes that enable them to digest plant cell walls from fungi and bacteria (14).

In the human ancestry there is evidence that an exchange of genes through interbreeding between different hominid lineages facilitated adaptation of populations to different climatic conditions. Denisovans and present-day Tibetans have similar alleles at an *EPAS1* gene that help them to cope with low oxygen levels at high altitude. The similarity is possibly due to gene exchange between Denisovans and early humans through interbreeding (15).

Introgressive hybridization does more than mix genes. It has the potential to produce offspring with phenotypes that lie outside the range of either parental species—a phenomenon termed transgressive segregation. The resulting individuals may colonize novel habitats where neither parental lineage can survive, as in the colonization of salt marshes by the sunflower *Helianthus paradoxus* (16). Much less understood, but potentially highly important, is the release of hidden variation when organisms enter a

new environment. A rare and clear example is Rohner *et al.*'s study of the blind Mexican cave fish (*Astyanax mexicanus*) (see the photo). In surface populations, the heat shock protein HSP90 masks variation for eye size. This variation is exposed in the altered conductivity of cave water and becomes available for selection (17). With the use of newly available research tools, we expect to see many more investigations of the release of cryptic variation in new environments.

Future genomic and ecological research on natural populations will provide a more comprehensive answer to Darwin's question of why the world is so extraordinarily rich in numbers, diversity, and complexity of organisms. Foremost among current questions is how gradual climate change and extreme climatic events cause rapid evolutionary change, and why some species groups diversify prolifically while others do not. ■

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10.1126/science.aam6411

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*Science* **355** (6328), 910-911. [doi: 10.1126/science.aam6411]

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