# SPECIATION AND INTRA-SPECIFIC TAXA

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**Summary**

The way one views speciation and the status of intra-specific taxa depends on the species concept adopted, but most of the literature is based on the early thinking on

species by Mayr and Wright. Conventionally understood speciation is typically thought to be a slow event, accomplished over a few million years. However, there are many examples of rapid speciation that have taken place over centuries or, as in many plants, within the time-frame of one generation. An understanding of speciation can be approached using population models that view the genetic structure of populations as being molded by forces of natural selection, balance between selection and habitat changes and selective forces acting upon small numbers of individuals. A number of modes of speciation, on the other hand, have been suggested by taking into account the effects of reproductive isolation on populations. Amongst these, geographic isolation (allopatric mode) best accommodates the recognition of intra-specific taxa, such as sub-species and semi-species, albeit such recognition lacks objective criteria. Chromosomally mediated reproductive isolation and speciation has been documented in a number of mammals and many angiosperms, but does not apply to all cases of speciation. Hence, a universal speciation mechanism has not yet been identified nor has a universal speciation mode been recognized. Each of the available modes and mechanisms of speciation probably applies to different environmental conditions. A thorough understanding of speciation, therefore, rests on multidisciplinary analyses of all possible contributing factors such as organism, molecular, chromosomal and habitat diversities.

## 1. Introduction

The history of life on Earth is one of multiplication of species, and this has resulted in a remarkable diversity of biological forms. Hence speciation, conventionally understood as the formation of new species, assumes a pivotal role in explaining biodiversity.

The crucial event in the origin of a new species is the absence of gene flow between populations which, within the framework of some species concepts, is referred to as reproductive isolation. Reproductive isolation is conceptually convenient to facilitate clear thinking of speciation modes and mechanisms, but can be applied comfortably only to biparental organisms such as most vertebrates as well as many invertebrate and plant taxa. Therefore, although this article focuses on speciation from the viewpoint of the biological species, the concepts discussed here may not be consistent with speciation of micro-organisms and organisms whose reproduction does not conform to this mode. To understand how a new species comes into existence, we need to understand how a barrier to interbreeding can evolve between the new species and its ancestor. By the same token, in order to demonstrate a lack of gene flow, we need to be informed of the genetic composition of the populations concerned. Such information is eminently supplied by measurements of genetic variation using methods typical of various disciplines such as biochemistry, cytogenetics, and molecular biology, amongst others.

One of the basic problems of biology concerns how discontinuities (such as those between closely related species) result from the essentially continuous process of evolution. Darwin's earlier notes and papers emphasized the importance of geographical isolation in the process of speciation, a fact driven home to him—in March 1837 after the voyage of the *Beagle*—by John Gould's observations concerning distinct species of mockingbirds (*Mimus*) occupying different islands of the Galapagos Archipelago. However, according to Ernst Mayr, Darwin's later writings (1850s

onwards) became preoccupied with explaining the origin of species on continents, where geographical barriers are less obvious, and he leaned towards ecological explanations for species formation, without requiring the presence of geographical barriers. Darwin's view of species as somewhat arbitrary "varieties" which underwent gradual transformation into new varieties probably contributed towards his acceptance of a process of gradual ecological divergence which did not require geographical isolation. In 1872 Darwin argued against his contemporary, Moritz Wagner:

*"I can by no means agree* [with Wagner] *that migration and isolation are necessary elements for the formation of new species ... I believe that many perfectly defined species have been formed on strictly continuous areas".*

This notion of "sympatric speciation" was widely accepted as prevalent in nature by Darwin's followers, but it took others such as Wagner, Rensch, Jordan, Dobzhansky and Mayr, to establish the universal importance of geographical isolation to the process of reproductive isolation and speciation. Indeed the neo-Darwinian paradigm of speciation is that of allopatric speciation: speciation that requires geographical isolation.

More than a century after Darwin's publication of *The Origin of Species*, evolutionary biologists are still actively debating the relative importance in nature of allopatric *versus* non-allopatric, that is sympatric and parapatric, modes of speciation. The possibility that reproductive isolation may be perfected by natural selection acting in hybrid zones formed on secondary contact of allopatric populations (the theory of reinforcement) is highly contentious. Speciation theory is beset with controversial ideas and sharply opposed alternative viewpoints, e. g. concerning the adaptive nature of speciation, the relative roles of natural selection and genetic drift, the possibility of "founder-effect" (peripatric) speciation, and the role of chromosomal changes in speciation.

Genetic analysis has contributed enormously to modern theories of speciation, by explaining the genetic basis of reproductive isolation, testing the validity of alternative speciation modes, and predicting the most likely speciation mode for different "genetic architectures" of species.

## 2. Time frame for speciation

While palaeontologists typically measure speciation over many millions of years, studies of extant species suggest that speciation, although usually gradual, can be rapid. Reproductive isolation can be induced in fruit flies (*Drosophila*) in the laboratory over a few generations. Diverse monophyletic "species-flocks" of cichlid fish occupying different African great lakes, have speciated in a surprisingly short period. Evidence from island-endemic species of cichlid fish in Lake Malawi, where these islands were part of dry land not much more than a century ago, suggests that these species originated in the past 100 years or so. It may be that strong sexual selection accelerates speciation, since very high species richness is often associated with strong sexual selection, such as the elaborate courtship displays found in birds of paradise (Paradisaeidae: 42 species, almost all occurring on one island, New Guinea). Speciation in plants may also be rapid. Most of the estimated 8 000 plant species occurring in the Cape Floristic Region of South Africa have evolved during the past 5 million years,

leading some botanists to postulate, recently, an "ecological" mechanism of speciation for the radiation of several plant genera of this region.

## 3. Ecological considerations

Mayr has remarked that "*there is no geographic speciation that is not at the same time ecological speciation and genetic speciation*". Ecological shifts and ecological selection typically accompany geographical isolation of populations, especially in the case of islands or small founder populations occupying new habitats that are marginal to the parent population. Ecological selection will result in genetic divergence, which in turn may result in pleiotropic effects on reproductive isolation. According to the recognition concept of species, habitat shifts may cause changes in the co-adapted male-female specific mate recognition system, leading directly to pre-zygotic isolation.

A concrete example where ecological selection directly causes reproductive isolation is known from Peter and Rosemary Grant's lifelong work on Darwin's ground finches (*Geospiza*) of the Galapagos Islands. Beak size and shape are adapted to the seed diet of this genus to an amazing degree. Overlapping diet between isolated species, strongly correlates with similar beak shape whereas, co-existing species on the same island differ in beak size and diet. Mate selection is based on bill size and, under experimental conditions, males fail to court stuffed females of the "wrong" beak size or shape.

Whether ecological differences alone can drive speciation in the absence of geographical isolation—as supposed by Darwin—is controversial, although modern theories of sympatric and parapatric speciation propose just this. Very low dispersal distances and the presence of very steep ecological gradients are regarded by some, as key factors accounting for the floral species diversity of the Cape Floristic Region. Hence "ecological theory" rather than geographical isolation, is being argued as the most likely mechanism of speciation within this biome.

## 4. Genetic models of speciation

### 4.1. Speciation by natural selection

Dobzhansky and Muller developed, in the late 1930s, a simple two-locus genetic model of reproductive isolation to account for the origin of post-zygotic isolation between two geographically isolated, adaptively diverging populations. In this model, isolation arises as an incidental by-product of adaptive divergence. An ancestral species of genotype $A_1A_1B_1B_1$ evolves to $A_1A_1B_2B_2$ in one population (due to stabilizing selection for that environment), and $A_2A_2B_1B_1$ in another (under stabilizing selection for a different environment). Speciation would result if epistatic interactions between the $A_2$ and $B_2$ alleles caused complete sterility or non-viability of hybrids. In this case, hybrid inferiority evolves between species without ever appearing within species: neither species need cross an "adaptive valley" (see figure 1B). While the general model is best interpreted against a background of natural selection acting on phenotypic characters, it can also be used to explain allelic substitution by random genetic drift, although genetic drift is usually associated with small populations (see figure 1A). This model can also be used to explain sexual selection, involving interaction between genes affecting male characters and those affecting female preference.
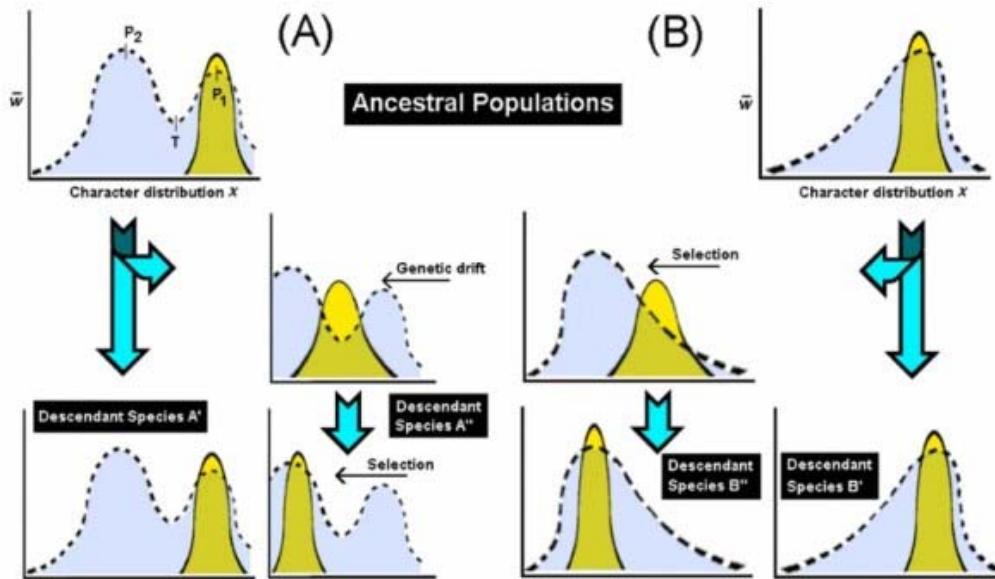
Figure 1. Speciation by peak shift (A) and adaptive divergence (B). Solid curve represents the distribution of character *x*; broken curve represents the relation between mean allele frequency of *x* and mean fitness (*w*). (A) Both speciating populations occupy a similar environment, but in A'' allele *x* evolves by genetic drift past the adaptive trough or valley (T) and then, by selection to another adaptive peak ($P_2$). (B) One speciating population, B'' occupies a changing environment and the frequency of x evolves to a lower value by selective pressure thus resulting in divergence that confers reproductive isolation.

According to Coyne, empirical demonstration of the above model, i. e. evidence that reproductive isolation can arise as an incidental by-product of adaptive divergence, is surprisingly scarce. Such evidence is limited to just two laboratory studies and one from nature, involving the evolution of copper-tolerant alleles in a mine dump population of the monkey flower (*Mimulus guttatus*) which are lethal in inter-population hybrids with neighboring populations.

## 4.2. Wright's shifting balance theory

The genetics of speciation, especially founder-effect models, is ultimately based on Sewall Wright's shifting balance theory of evolution, proposed in 1931. This theory uses the metaphor of an adaptive landscape to depict variation in fitness between genotypes in a population. This landscape is three dimensional, with a plane of gene combinations being contoured with fitness values, where peaks represent high fitness and valleys low fitness (see figures 2 and 1A).

With changes in the environment, peaks and valleys may move relative to populations. While stabilizing selection forces a population towards the nearest peak, genetic drift may cause a population to override selection and move away from the peak. Similarly, subdivision of a large population into small semi-isolated demes, can overcome the effects of stabilizing selection. A peak shift—across an "adaptive valley" —represents a speciation event (see figures 2B and 1B). Alan R. Templeton provides a useful analogy for understanding how selection and drift can act together in producing adaptive

evolution and speciation. By hypothetically inverting the adaptive landscape surface, so that peaks become valleys and valleys peaks, and by imagining demes to be balls, selection acts like gravity, causing the balls to fall into the nearest hole (adaptive peak). Drift is analogous to someone physically shaking the surface from side to side, causing balls to roll out of their holes and into other nearby holes.
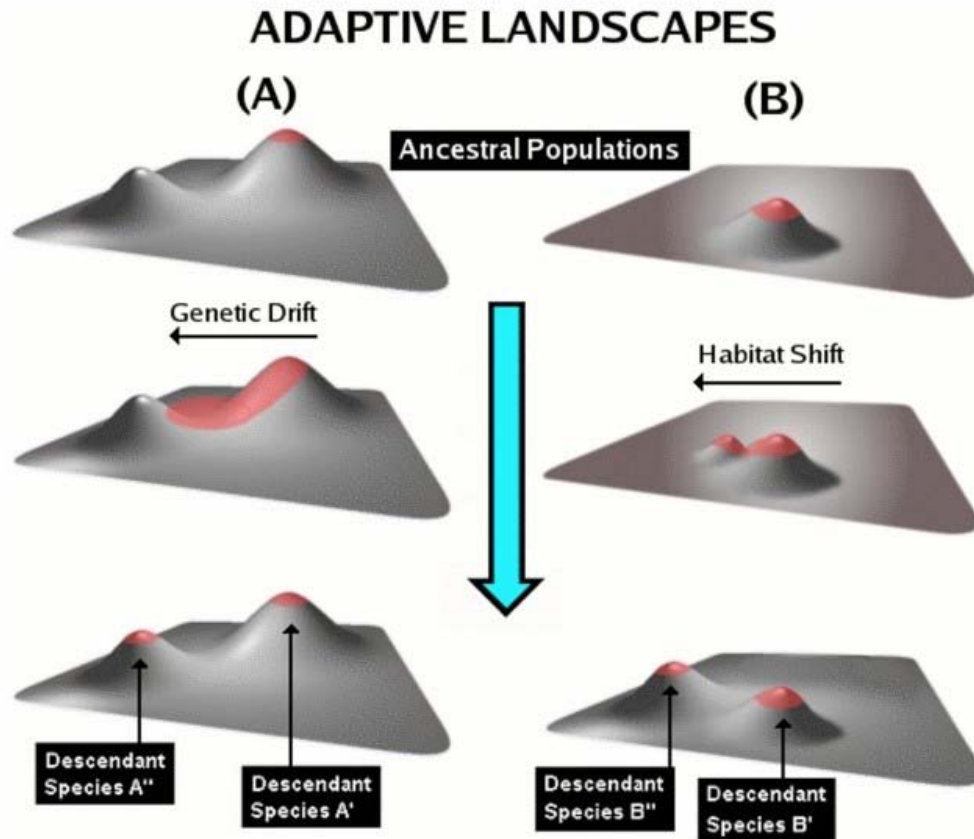


Figure 2. Shifting balance illustrated by adaptive landscapes

## 4.3. Founder-effect models

All following models of speciation by founder-effect share the concept of random drift establishing new gene combinations, which are then acted upon by selection.

From 1942 onwards, Mayr developed the basic idea of founder-effect speciation whereby a small number of individuals separated from the parent population, undergo a rapid loss of genetic variation, i. e. increased homozygosity, due to drift and inbreeding and selection acts against deleterious combinations in homozygotes. These conditions are hypothesized to facilitate radical changes in the genome due to epistatic effects, and the formation of new gene combinations which are subjected to novel selection processes. This radical process was termed "genetic revolution" by Mayr, and underpins Mayr's concept of peripatric speciation (see figure 2). These conditions of small population size and random drift allow the chance fixation of chromosomal rearrangements resulting in inferior hybrids which would otherwise be removed by selection. In this way, post-zygotic isolation, through hybrid dysgenesis and potentially

speciation, can be acquired rapidly in peripatric isolates.

Two variants of this model have been presented by Carson and by Templeton, respectively.

Carson's flush-crash-founder model also requires a population bottleneck as shown in figure 3, but does not envisage reduced genetic variation associated with this. The model predicts population growth associated with favorable environmental conditions, resulting in relaxed selective pressure. Under relaxed selection, new combinations of strongly epistatic genes are produced which would be selected against in the ancestral population. This stage is followed by a population crash (bottleneck) leading to near-extinction of the population, with just a few survivors bearing new gene combinations occurring in high frequencies as the population subsequently increases and a new selective regime is imposed.
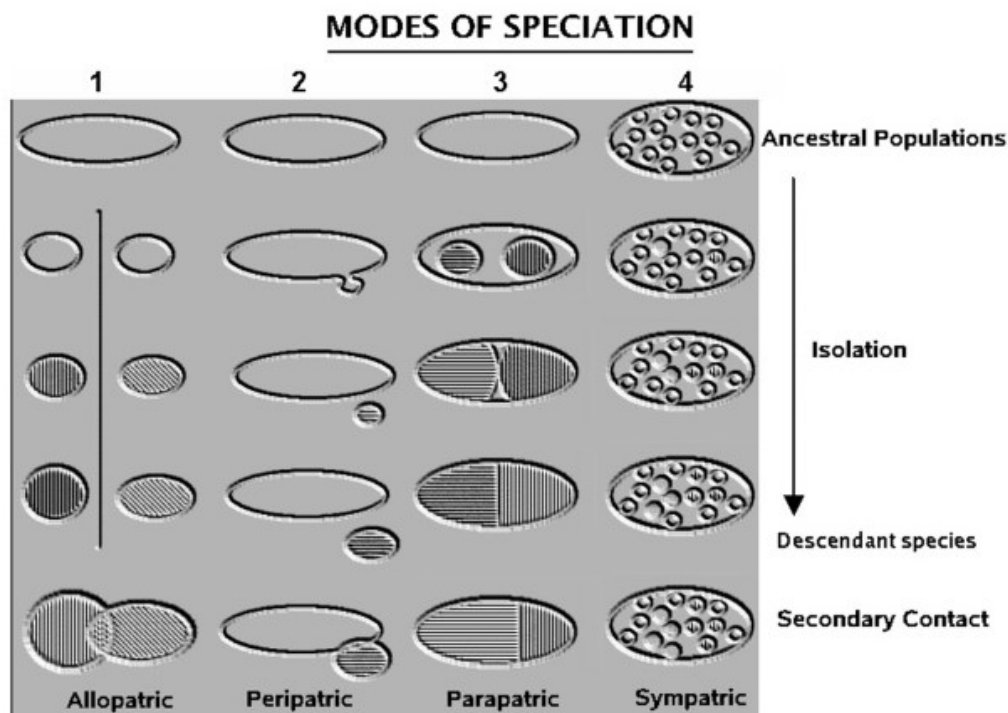


Figure 3. Diagram of speciation modes

Unlike Mayr's theory, which is primarily concerned with stochastic fixation of alleles and/or chromosomal rearrangements, Carson's model views the major effect of the founder event as being the disruption of the homeostatic, co-adapted "closed system" of the parental species. This disruption would lead to major changes in polygenic balances affecting integrated developmental, behavioral and physiological traits. Disorganization of the parental genome is regarded as necessary for the subsequent reorganization under the new selection regime. A variation of the flush-crash-founder model is the founder-flush model which postulates a flush following, rather than preceding, a founder event.

The genetic transilience model of Templeton, differs from Mayr's model in that founder events do not trigger genome-wide genetic "revolutions" but, rather, more subtle changes at few major gene loci and their epistatic modifiers. Variation remains high

throughout the bottleneck but, abrupt changes occur in allele frequencies of such few major genes resulting in strong selection on the modifier genes.

Some evidence exists for genetic reorganization, from experimental bottlenecks induced in laboratory colonies of flies. The patterns of endemism in the diverse monophyletic lineages of *Drosophila* in the Hawaiian Archipelago provide circumstantial evidence for speciation associated with founding events on islands. For example, the common pattern of single-island endemism, with sister species of endemics occurring on adjacent islands, strongly indicates that speciation is associated with colonization of an island.

## 4.4. How many "speciation genes"?

The standard genetic model of reproductive isolation discussed in Section 5.1, assumes a minimum of two genetic loci to be necessary for speciation to occur. The classical neo-Darwinian viewpoint assumes that isolating factors are polygenic, a conclusion supported by experimental studies in *Drosophila*. Also, at least 150 genes are thought to have been responsible for the non-viability of hybrids between two chromosomal races of the grasshopper *Podisma pedestris*. At the other extreme, pre-zygotic isolation in snails is apparently caused by single mutations that change the direction of the coiling, making copulation impossible. In the corn borer, ethological isolation is caused by changes in sex pheromone production and perception mediated by three genes.

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**See also Bibliography for *Species Concepts*.**

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**Biographical Sketches**

**Peter John Taylor** was born in January 1963. A Zimbabwean citizen by birth, married with four young children, Peter Taylor obtained his B.Sc. from the University of Cape Town in 1983, with Zoology and Botany as majors. His B.Sc. (Honours), also from University of Cape Town, was obtained in 1984. His Ph.D., on "Infraspecific systematics of the yellow mongoose (*Cynictis penicillata*)", was obtained from the University of Natal Durban in 1990.

Peter Taylor was a volunteer/student at the Mammal Department of the Transvaal Museum and later Scientific Assistant to the late Prof. J.A. Meester, at the University of Natal. He took up his present post as Curator of Mammals at the Durban Natural Science Museum in July 1989. His research at the Museum is centered on the evolution, classification and conservation of small mammals including vlei rats, bats, shrews and mongooses.

Peter Taylor has published 48 scientific papers and 10 popular science articles since 1985 and presented scientific papers at six overseas conferences (in Britain, Rome, Israel, Brazil, Australia and France), as well as at several local conferences. His book on "The smaller mammals of KwaZulu-Natal" was published by University of Natal Press in 1998, and a full color popular field guide on "Bats of Southern Africa" was published in November 2000. He belongs to the Wildlife Society of Southern Africa, the Zoological Society of Southern Africa, the Natal Evolutionary Biology Society and the Southern African Museums Association (Natal Branch).

Peter Taylor founded the Durban Bat Interest Group (DBIG) in February 1994. The group currently numbers some 150 individuals, and was nominated for the "Conservationist of the Year" award by the KwaZulu-Natal Nature Conservation Service.

**Giancarlo Contrafatto**, born 1948, is a graduate in Biological Sciences from the University of Turin (Italy) and obtained his Ph.D. from the University of Natal Durban (South Africa). His research interests are isolation mechanisms related to speciation of small mammals. Recipient of the 1976 British Association Medal from the South African Association for the Advancement of Science. G. Contrafatto has been on the staff of the University of Natal since 1983, and is responsible for the courses of Microbiology, Immunology, Comparative Immunology, Systematics and Evolution.