

# Sympatric Speciation

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*Based in part on the previous version of this Encyclopedia of Life Sciences (ELS) article, Speciation: Sympatric and Parapatric by Michael G Ritchie.*

**Sympatric and parapatric speciation refer to the origin of biological species in the absence of complete geographic isolation between the diverging taxa. Until recently, most biologists believed that geographic isolation was almost universal in the development of species, i.e. most species originated in allopatry. However, new empirical and theoretical studies have shown that speciation may occur despite the diverging populations having adjacent or overlapping geographic ranges and despite on-going gene flow. Attention in speciation studies has shifted to the mechanisms responsible for reducing gene flow, regardless of the extent of geographic range overlap.**

That was a very interesting story. But I don't believe it. Sympatric speciation is like the measles: everyone gets it, but they all get over it.

Theodosius Dobzhansky, sitting on the committee examining Guy Bush's PhD thesis on sympatric speciation in apple maggot flies in 1968.

## The Geographic Modes of Speciation

The process of speciation has traditionally been subdivided according to the geographical context in which it occurs, into sympatric, allopatric and parapatric modes. The distinguishing difference between these is the geographic overlap between the speciating populations, which is respectively complete, limited to the edges of the population ranges, and non-existent.

The most controversial of the three geographic modes of speciation has been sympatric speciation. The problem is that gene flow, which can be excluded in allopatric scenarios and is limited in parapatry, is presumed to exist in sympatry because of the physical proximity of the

**ELS subject area:** Evolution and Diversity of Life

### How to cite:

Veltsos, Paris; and Ritchie, Michael G (May 2011) Sympatric Speciation. In: eLS. John Wiley & Sons, Ltd: Chichester.  
DOI: 10.1002/9780470015902.a0001749.pub2

## Advanced article

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Online posting date: 16<sup>th</sup> May 2011

diverging populations. Gene flow opposes divergence at individual loci, and can reverse pre-existing divergence of two sympatric populations by allowing recombination between their loci, breaking down any polygenic barriers to interbreeding they may originally contain, thus stopping speciation (Felsenstein, 1981).

Coyne and Orr have suggested four criteria that must be satisfied before a speciation event can be concluded to have occurred in sympatry. Two species will have originated sympatrically if (1) their current distribution is sympatric, (2) they form a monophyletic group, (3) they are completely reproductively isolated and (4) past allopatry can be ruled out (Coyne and Orr, 2004). Few, if any, examples successfully satisfy all these criteria. Furthermore, in many systems it may simply be impossible to exclude condition (4). The most likely cases to rule out allopatric speciation are small, isolated volcanic islands or crater lakes, whose emergence time can be provided by radioactive isotope dating. Even then scenarios involving double invasions or 'micro-allopatry' within a habitat are difficult to eliminate completely. **See also:** [Speciation: Introduction](#); [Species and Speciation: An Overview](#)

## From modes to mechanisms

The division of modes of speciation according to geography has led to important insights, such as the focus on the relative importance of environmental (external) versus genetically induced (internal) isolation. However, focusing on processes currently generating isolation seems more suited for speciation studies, because speciation itself is a long-term process during which different mechanisms can become important at different times. For example it is possible that a sympatric stage is required to complete speciation through reinforcement, but reinforcement itself may occur in response to incompatibilities that have arisen in allopatry (see reinforcement). A modern view could replace the strict geographic modes of speciation with the role of geographic separation in divergence, at different points in time.

The emphasis on geographic modes of speciation is also not justified by the type of data typically used in speciation studies. In practice, when one studies speciation the main interest is the mechanisms that allow divergence. Indeed a shift in focus from whether a case fits a particular

geographical scenario to the actual biological processes that can be evaluated with current data characterises recent studies of speciation (Butlin *et al.*, 2008; Fitzpatrick *et al.*, 2008; Sobel *et al.*, 2009). Viewed in the light of processes allowing divergence, the main difference between sympatric and allopatric speciation is that in allopatric cases no special mechanism for divergence is required, as the lack of gene flow ensures differences will accumulate even by drift. In contrast, in sympatric cases there must be some process that limits gene flow in addition to any selected or non-selected process that generates divergence. **See also:** [Isolating Mechanisms](#); [Species Concepts](#)

## Sympatry in terms of gene flow

The strictest definition of speciation in sympatry (or parapatry) is the one requiring gene flow. Cases when the potential for gene flow does not manifest to actual gene flow, perhaps because of niche differentiation, are termed 'micro-allopatric' and may not be considered 'true' sympatric speciation. The focus on gene flow may be characterised as pedantic, but it is important because of its central role in theoretical models of sympatric speciation.

## Models of Speciation

Early models (the most influential being those of Maynard Smith and Felsenstein) emphasised the great difficulty of obtaining speciation in sympatry. The problem is that it is difficult to create and maintain linkage disequilibrium between alleles conferring increased fitness in different habitats and those that generate assortative mating. If stable and complete linkage disequilibrium was maintained, ecological adaptation would have led to complete divergence and potential speciation. Assortative mating genes could either be alternative alleles at a single locus or, more realistically, separate genes for male indicator traits and female preferences. Any cases where assortment is less than perfect or the fitness of hybrids greater than zero result in scrambling of the favoured multilocus genotypes at each generation owing to independent segregation and recombination among the loci involved. **See also:** [Adaptation and Natural Selection: Overview](#); [Population Genetics: Overview](#); [Species Selection](#)

Felsenstein produced a simple three locus model (Felsenstein, 1981), which was widely influential. It failed to produce speciation in the absence of very strong selection against biallelic gene combinations favoured in different habitats (a third locus influenced assortative mating). Even such a simplified model with an unrealistically small number of loci influencing speciation failed to produce sympatric speciation owing to recombination. Recombination breaks down non-random associations between alleles at different loci (termed linkage disequilibrium), stopping or reversing any divergence between populations with different alleles associating. The situation is even worse for traits determined by several genes, as it

would be more difficult to crystallise adaptive gene combinations. **See also:** [Linkage and Crossing over](#); [Population Genetics: Multilocus](#); [Quantitative Genetics](#)

Diehl and Bush (1989) incorporated into the Felsenstein model the idea that assortative mating arises as a byproduct of habitat choice. In this case natural, rather than sexual, selection might favour sympatric speciation, by influencing habitat choice. Resource exploitation was modelled as the product of two unlinked loci (similar to hybrid dysfunction in Felsenstein's model), while a third locus influenced migration to a habitat or resource in which mating takes place, rather than assortative mating. The habitats could be made effectively sympatric by changing the level of migration. Under relatively modest selection intensities ( $s=0.1$  or  $0.3$ ) disequilibria were maintained between a stable polymorphism at the migration locus and the loci influencing resource exploitation, despite the three loci being unlinked. The main criticism of the model by sceptics was that the strong habitat choice involved was effectively making the organisms behave as though they were not in sympatry. **See also:** [Fitness](#); [Genetic Load](#)

A quantitative genetic approach to modelling sympatric speciation followed. The emphasis here was on phenotypes, rather than genotypes, which avoided the geometric expansion of gene combinations necessary in previous models. Emphasis shifted to the fitness of individuals with a particular phenotype, assuming that all genotypes that could result in this phenotype are equally common. This is equivalent to assuming that all genes have the same allele frequencies, and are unlinked. Trait evolution in subsequent generations could then be calculated (Kondrashov and Mina, 1986; Kondrashov and Kondrashov, 1999).

In the simplest model, an organism is subject to disruptive selection on a trait involved with resource exploitation, for example body size. Disruptive selection leads to bimodality for the trait through frequency-dependent competition. There is also a phenotypic trait that influences assortative mating (e.g., colour, with individuals showing positive assortment). Linkage disequilibrium deterministically builds up between some combination of resource exploitation and assortative mating traits (in real organisms drift may help establish an initial covariance). Intermediate individuals form rarely, and those that do are removed by selection. Kondrashov and Kondrashov (1999) describe this process as the 'recruitment' of colour to provide reproductive isolation between individuals of different body sizes. The process, which is akin to reinforcement, still occurs if assortative mating is determined by independent genes for male traits and female preferences. **See also:** [Adaptation: Genetics](#); [Character Displacement](#); [Drift: Introduction](#); [Reinforcement](#); [Speciation: Genetics](#)

## Isolation owing to single genes

An interesting theoretical development is the possibility of 'magic traits'. The term was coined by Gavrillets (2004) to describe traits simultaneously experiencing natural selection (disruptive or divergent) and contributing to

assortative mating and have also been called ‘one-allele’ systems (Rice and Hostert, 1993; Ortiz-Barrientos and Noor, 2005). Magic traits are immune to the recombination that leads to breakdown of the coadapted genotypes responsible for isolation between populations. For example, adaptation to a feeding site, which is also used as a breeding site, can be controlled by a single locus and can be sufficient to result in isolation between individuals that carry different variants of that gene. The general prevalence of magic trait genes is unknown in nature. Among the most famous cases is the apple maggot fly, where host plant preference influences feeding and mating (Bush, 1969). Similarly, the sizes and shapes of beaks in Darwin’s finches may influence both courtship song and trophic niche (Grant and Grant, 1979; Huber *et al.*, 2007). **See also:** [Darwin’s Finches](#)

Another theoretical possibility is for specific alleles to contribute to assortative mating, by signalling local adaptation. Many condition-dependent sexually selected traits may function this way: only locally adapted males will be capable of successfully expressing the sexually selected trait in question. Any females choosing the male morph not adapted to its environment will suffer a fitness cost through its offspring, leading to disruptive selection (van Doorn *et al.*, 2009).

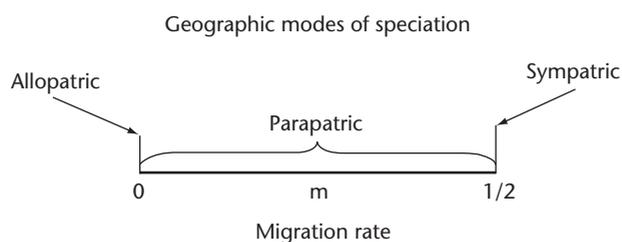
Both magic trait (one gene, multiple alleles) and ‘one-allele’ models can lead to speciation in a greater range in the parameter space than two-gene models.

## Adaptive dynamics

The recently developed field of adaptive dynamics simplifies the underlying genetics, by assuming one substitution happens at a time, and places its emphasis on phenotypes. This allows relatively simpler modelling of the ability of different phenotypes to invade different ecological niches, which may occur in sympatry. Adaptive dynamics has demonstrated the potential for evolution of branching points arising out of simple, common ecological scenarios, such as competition and predation (Dieckmann and Doebeli, 1999; van Doorn *et al.*, 2004).

## Theoretical conclusions

Speciation in sympatry seems possible under some assumptions, especially when genetic architecture reduces recombination between influential loci. The next step is to test whether real species in nature adhere to such assumptions. Early models suggested that sympatric divergence was easier under natural, rather than sexual, selection. However it is becoming apparent that perhaps the greatest potential for divergence exists when there is interplay between the two. **See also:** [Adaptation and Natural Selection: Overview](#); [Cultural Transmission and Evolution](#); [Natural Selection: Introduction](#); [Sexual Conflict](#); [Sexual Selection](#)



**Figure 1** Geographic modes of speciation, according to gene flow. Reproduced with permission from Gavrilets (2003).

## Examples of Sympatric Divergence

The geographical localisation of populations is not stable during the time it takes for speciation making it difficult to rule out allopatric stages. In addition, sympatry and allopatry are extreme points in a continuum of possible gene flow (Figure 1). Describing mechanisms of divergence are more tractable and biologically relevant questions, and provide insights to whether sympatry contributes to or eradicates differentiation.

With these considerations in mind, we present some examples where divergence seems to persist or increase in sympatry.

## Ecological differentiation

### Apple maggot flies – host-parasite coevolution

The apple maggot *Rhagoletis pomonella* is perhaps the classic case of sympatric speciation. The natural host in which the maggots develop are fruits of hawthorn, but in the last 150 years its host range has expanded to include cultivated apples. Guy Bush studied these organisms for his PhD. He realised that a single behavioural attribute, host plant preference, is a potential magic trait, since it also indirectly affects courtship, mating and oviposition. Furthermore, different plant phenologies, particularly fruiting time, might lead to a build-up of genetic differences between host races.

Bush argued that, because of the divergent selection on new host plants and consequential assortative mating, geographic isolation was not necessary for speciation (Bush, 1969). As performance on a plant species evolves, a broadly polyphagous insect might evolve into a complex of sympatric specialist species, provided that different host plants occur in sympatry. In support, neutral genetic markers showed approximately twice the genetic distance between flies from different and flies from the same host plant (see Barton *et al.*, 1988, for a summary). Evidence for host fidelity (Dambroski *et al.*, 2005) and differences in developmental period (Filchak *et al.*, 2000) were also obtained, making *R. pomonella* a celebrated example of divergence in sympatry.

This apparently straightforward case of sympatric divergence turned out to be more complicated. Evidence for a secondary invasion was recently uncovered, suggesting that genetic differentiation important for host

fidelity arose in allopatry (Feder *et al.*, 2003; Xie *et al.*, 2007). Importantly, the genetic regions involved with host fidelity localise on chromosomal inversions, protecting them from recombination when different sympatric forms hybridise. **See also:** [Molecular Ecology](#); [Variation, Within Species: Introduction](#)

*R. pomonella* now serves as an example of the difficulty to rule out non-sympatric contributions to isolation. It is also a good illustration of the complexity that gives rise to isolation: historical and genetic factors were involved in the sexual and natural selection that, to this day, has stopped the host-specific forms from merging into a single species. **See also:** [Coevolution: Plant–Insect](#)

### Lacustrine fish – trophic niche adaptation

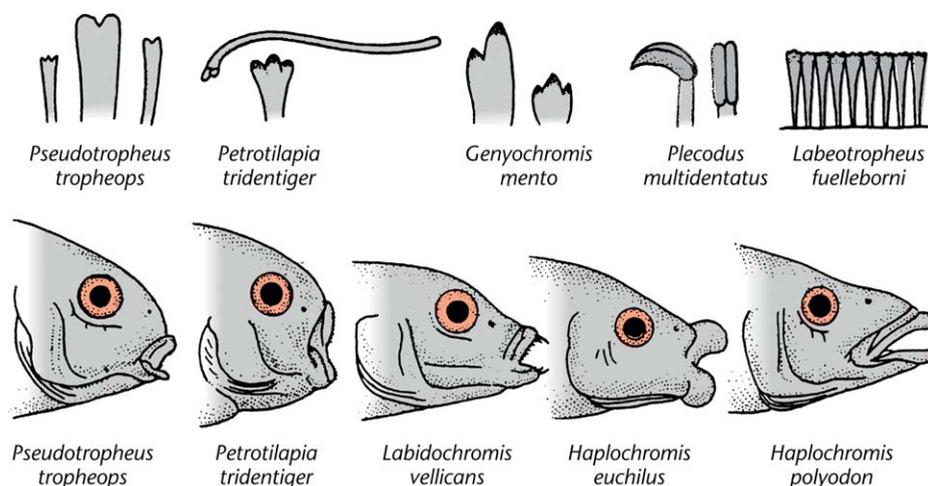
Past allopatric distributions are easier to exclude in lacustrine (lake-dwelling) fish. Genetic and behavioural studies have produced compelling evidence for extremely rapid adaptive radiation and speciation within the relatively confined habitats of lakes. In particular, the cichlid species endemic to the major African lakes of Malawi, Tanganyika and Victoria have been subject to extensive taxonomic revision and study. Firstly, divergence in colour patterns often associated with courtship point to the importance of sexual selection in generating assortative mating between forms. Many who previously thought to represent colour polymorphisms are now thought to be species isolated by sexual behaviours. Reviews estimate that the above lakes have as many as 1000, 200 and 500 endemic cichlid species respectively (Turner, 1999; Seehausen *et al.*, 2008). Also, there is often an association with trophic specialisation, with each species having divergent mouthparts, so reducing interspecific competition for resources by specialising on different food types (**Figure 2**). Phylogenetic analyses of DNA markers suggest that the fishes of each lake are monophyletic. Lake Malawi is only around 1–2 million years old, and Lake Victoria perhaps only tens of

thousands of years old, so these fish species have undergone extremely rapid speciation. The mean ‘speciation interval’ calculated for these species can be as low as tens of thousands of years (Turner, 1999). This is much faster than anything described elsewhere, in fact Coyne and Orr (2004) describe their speciation interval as ‘almost beyond belief’.

Could the rapid speciation of these fish be sympatric in origin? It is not possible to rule out that the lakes provide sufficient diversity in habitat, particularly around rocky shores and during fluctuations in water level, for species to have undergone effectively para- or allopatric speciation within the lakes. However, this seems unlikely, particularly as DNA markers suggest strong monophyletic origins of geographically closely associated species. It is thought more likely that divergent selection for resource exploitation and sexual selection have together selected for the origin of these species despite on-going gene flow. Detailed studies of sticklebacks from North America and Iceland (Schluter and McPhail, 1992; Ólafsdóttir *et al.*, 2007) charr from arctic lakes (Castric *et al.*, 2002) and cichlids in crater lakes in Nicaragua and elsewhere (Wilson *et al.*, 2000; Schliewen *et al.*, 2006; Barluenga and Meyer, 2010) have suggested that a similar process of sympatric lacustrine speciation can occur in non-African lakes. **See also:** [Adaptive Radiation](#); [Interspecific Competition](#); [Lake Communities](#); [Lake Ecosystems](#)

### Direct influence of environment

One of the least disputed cases of sympatric speciation is palms on Lord Howe island (Savolainen *et al.*, 2006; Babik *et al.*, 2009). The island is geographically isolated from any other landmass, which could have provided forms diverged in allopatry. Divergence time between two endemic species, estimated from molecular markers, place speciation after the island was formed. No polyploidy is involved (which is a valid, but easy way to achieve sympatric speciation and is often ignored (see polyploidy below)), most of the genome



**Figure 2** Adaptive radiation of feeding specialisations among African lake cichlids. Diet and mode of feeding profoundly influence both head and tooth shape. Reproduced with permission from Futuyma (1998) *Evolutionary Biology*, 3rd edn, Figure 5.30, p. 119. Sunderland, MA: Sinauer. Copyright © 1998.

is not differentiated between the two species (i.e. other differences have not accumulated in an allopatric stage) and there is reproductive isolation between the species, based on flowering time, which is associated with the substrate on which the palms grow. The endemic palm trees of Lord Howe island are thus a good example where differentiation persists despite the potential for gene flow, since the trees occur in a very small area and are wind pollinated. **See also:** [Ecological Genetics](#); [Environmental Heterogeneity: Temporal and Spatial](#); [Molecular Phylogeny Reconstruction](#)

## Allochronic speciation

Temporal isolation of species occurring in the same geographic area is a potent force for divergence in sympatry. Typical characters involve flowering time in plants or breeding period in insects. Allochronic isolation may be easy to evolve because it can be achieved by rapid changes, perhaps in only a few loci. In some cases, allochronicity can be a consequence of habitat differentiation, as in the Lord Howe palms (Savolainen *et al.*, 2006; Babik *et al.*, 2009) and the grass *Anthoxanthum*, where adaptation relates to heavy metal tolerance (Silvertown *et al.*, 2005; Antonovics, 2006), or host plant phenology, as in *Enchenopa* (Wood and Guttman, 1983). Cases of genetic differences are less clear. One potential example are the green lacewings *Chrysoperla carnea* which may have originated in sympatry by relatively simple genetic changes affecting photoperiodic control of breeding period (Tauber and Tauber, 1977), though they also differ in habitat and courtship behaviours (Wells and Henry, 1994). **See also:** [Heavy Metal Adaptation](#)

## Reinforcement

Reinforcement is the evolution of reproductive isolation in sympatry or parapatry in response to the production of deleterious hybrids. These can arise owing to differentiation in allopatry or in a sympatric context. In the case of secondary contact, reinforcement is an example where a sympatric stage actively contributes to isolation but may not have initiated it. Perhaps not surprisingly, reinforcement has also been a controversial subject, but cases supporting it are now widely accepted.

The case for reinforcement is made in *Drosophila* using geographical distribution data (Noor, 1995). Populations of closely related species were shown to have stronger sexual isolation in sympatry. A sympatric stage thus appears to have helped advance speciation by generating selection for reduced gene flow. Interestingly, genomic regions associated with incompatibility have been mapped to chromosomal inversions in *Drosophila* (Noor *et al.*, 2001). These regions may thus counteract the negative effects of gene flow by preventing recombination. **See also:** [Character Displacement](#); [Chromosome Rearrangement in Evolution](#); [Reinforcement](#)

## Cultural differentiation

Learned behaviour with the potential to sexually isolate individuals is very interesting because it can initiate isolation rapidly, within a single generation. Parasitic songbirds provide an extreme example: juveniles learn and imitate the song of their foster parents. The same song is used by the adult males to attract females, who respond only to the song they were exposed to as juveniles. Consequently, if a female laid eggs in the nest of the wrong host species, her offspring would instantaneously be reproductively isolated from all other birds reared in the original host nests. Two cases are known in cuckoos where host race differentiation correlates with genetic differentiation, which presumably evolved later (Gibbs *et al.*, 2000; Starling *et al.*, 2006). Another case involves African indigobirds, where geographically overlapping genetically differentiated populations exist. Importantly, their divergence times are shorter than those of the host species, suggesting the differentiation occurred in sympatry (Sorenson *et al.*, 2003). The major criticism of this process is that the newly formed cultural groups can merge as easily as they are generated, since no genetic change is associated. In support, the speciation rate in such groups has been found to be higher, but this is also true of extinction rate, so that the net effect is neutral (Krüger *et al.*, 2009). Once more, a past allopatric phase cannot be ruled out.

## Polyploidy

The most widespread and least controversial form of sympatric speciation is through polyploidy, in which two parental genomes (of the same or different species) are combined into a new individual. Normally, the hybrid would be sterile because of abnormal chromosome pairing in meiosis. However normal meiosis can be restored if chromosome doubling takes place in the hybrid. The emerging polyploid individuals are fertile with each other but produce sterile hybrids with their parents, because of problems with meiosis. Polyploid speciation has sympatric origins because the original hybridisation must have occurred in sympatry (though geographic separation may contribute to the successful establishment of a polyploid). Polyploid speciation is common among plants, for example 15% of angiosperms and 31% of fern speciation events are accompanied by ploidy change (Wood *et al.*, 2009).

Despite the undoubted importance of polyploidy to plant speciation, among evolutionary biologists this has largely been considered an exception to the normal rule of allopatric speciation, an oddity which, by its mechanism, in a way illustrates the difficulties facing models of sympatric speciation that do not rely on equally simple, almost instantaneous, methods of producing reproductive isolation. **See also:** [Hybrid Speciation](#); [Plant Breeding and Crop Improvement](#); [Plant Reproduction](#); [Ploidy Variation in Plants](#); [Polyploidy](#)

## Speciation through hybridisation

Hybrids between species could become established without changes in chromosome number if they have fitness advantages, for example if the hybrids are fitter in intermediate habitats. This seems to be the case in some sunflower *Helianthus* species where some hybrids are better adapted to particular habitats (Rieseberg *et al.*, 2007; Rieseberg, 2009). Patchy or disturbed environments may be the most suitable for speciation through hybridisation. Hybrid genotypes may show overdominance for fitness in some habitats, or transgressive genetic variation released by hybridisation may contribute to adaptation. However, once more, spatial isolation from the parental species may still be required for hybrid establishment (Buerkle *et al.*, 2000).

Another avenue for hybrid speciation is that a specific hybrid trait may contribute to the success of a novel lineage. 'Hybrid trait speciation' has been proposed for *Heliconius* butterflies where the wing patterns of some natural populations found in regions of geographic overlap between species resemble those of laboratory hybrids (Naisbit *et al.*, 2001). The hybrid wing morph has a fitness advantage owing to frequency-dependent Mullerian mimicry (Mallet *et al.*, 1998). The trait can be considered a 'magic trait', because it can additionally contribute to assortative mating by being a target of mate choice (Mavarez *et al.*, 2006). **See also:** Adaptive Divergence in Sunflowers; Hybrid Zones; Mimicry; Selection: Frequency-dependent

## Conclusions

### The importance of geographic separation

Very few examples exist where the establishment, build-up and completion of reproductive isolation can be confidently shown to have evolved exclusively in the same geographical area in the face of on-going gene flow. It is particularly difficult, and often impossible, to exclude phases of allopatry that may have occurred in the past.

Empirical evidence backs up a central role of geographic isolation for speciation. For example, Kisel and Barraclough (2010) performed a meta-analysis comparing phylogenetic distance and migration capability of organisms spanning the tree of life. All were examples of within-island speciation, yet there was a strong correlation between the degree of mobility and island size, suggesting that some geographic isolation is necessary for genetic differentiation to evolve. Interestingly ferns, which speciate mostly due to polyploidy, did not follow this pattern. Other evidence suggesting that most differentiation arises in allopatry is provided by meta-analyses where population differentiation plotted against geographical distance (Barraclough *et al.*, 1998) does not support sympatric origins.

Although physical separation may be necessary to initiate divergence between populations in most cases, physical proximity may sometimes reinforce their divergence as

a response to selection against hybridisation. A sympatric stage may therefore be rare in initiating speciation, but more common in reinforcing or completing it. Limited cases, like the Lord Howe palms, where differentiation seems to have arisen in sympatry are also known. More cases of hybridisation or polyploidy, both of which must have occurred in sympatry, also exist and show that speciation may occur, and certainly progress, in sympatry. **See also:** Islands

### The complexity of speciation cannot be captured by the geographic modes of speciation alone

The study of speciation has revealed that reproductive isolation is the product of complex interactions between geography, genetics and different forces of selection. The focus in speciation studies is shifting towards understanding how these forces interact to result in reproductive isolation. Sympatric speciation best refers to these modern studies which attempt to understand divergence in the face of homogenising gene flow during some stage of the speciation process.

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