

Quick guide

Sympatric speciation

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What is sympatric speciation?

The likelihood of sympatric speciation is perhaps *the* most controversial aspect of speciation, and certainly one of the most contested questions in evolutionary biology. Speciation in general is defined as the evolution of strong, genetically based ‘isolating barriers’ between populations that prevent them from exchanging genes, for example, mate discrimination, habitat differences and hybrid sterility. *Sympatric speciation*, from the Greek ‘same place’, involves the splitting of an ancestral species into two or more reproductively isolated groups *without geographical isolation of those groups*. The key aspect of sympatric speciation is that it occurs when incipient species are in physical contact with each other, potentially able to interbreed and exchange genes.

How does it differ from other forms of speciation?

Sympatric speciation is unique because the process begins with complete genetic mixing between the diverging groups. Traditionally, most speciation was thought to require the physical isolation of populations by a geographic barrier — mountain, river, desert and so on— which, by completely preventing gene flow, allowed the populations to evolve independently. Eventually, these populations would develop isolating barriers as a byproduct of their divergent evolution. This process is called *allopatric speciation*. A related process, *parapatric speciation*, is the formation of species from populations that are somewhat but not completely geographically isolated, so that reproductive barriers begin to evolve when there is restricted gene flow.

How is sympatric speciation supposed to occur? The most common scenarios involve *disruptive selection*, that is, natural selection driving a population in two different directions at once. A population of herbivorous insects, for example, may be selected to use two very different types of plant growing in a single area. If this selection is strong enough, it can cause the population to divide into two subpopulations, each specializing on a different resource, with hybrids between the subpopulations suffering reduced fitness because they are not well adapted to either resource. Speciation can then occur if insects either mate exclusively on the resource they use (habitat isolation), or choose as mates only individuals using the same resource (sexual isolation). There are other forms of sympatric speciation involving disruptive selection on mate choice — for example, where females prefer different types of males — but the most plausible ones involve an initial partitioning of ecological space followed by the evolution of mate discrimination.

Why is sympatric speciation difficult to achieve? It’s hard to achieve because of the genetic recombination that occurs when incipient species interbreed. This recombination breaks up the correlation between co-adapted groups of genes that is necessary for species to form. For example, genes conferring adaptation to use of one resource might, through recombination, become associated with genes conferring behavioral preference for the other resource, or with genes for preferring mates using the *other* resource. Recombination between groups diverging in sympatry thus produces maladapted individuals, slowing down or preventing speciation.

Because recombination is so powerful at preventing sympatric speciation, the conditions under which such speciation can occur can be quite restrictive. Selection, for example, must usually be strong, and there are also restrictions on the number of genes that can contribute to differences in species-specific traits, and on their

linkage relationships to each other. In contrast, there are far fewer restrictions on allopatric speciation, which requires only that selection produce adaptive differences between isolated populations, and that reproductive isolation evolves as a byproduct of these differences. (Parapatric speciation is intermediate in difficulty.)

Why is sympatric speciation so controversial? To some evolutionists, especially those working on host-specific insects, sympatric speciation seems intuitively obvious and easy. Yet theoretical models show that it occurs only under conditions that appear restrictive and biologically unrealistic. Because it is difficult to get unequivocal evidence for sympatric speciation in nature (see below), evolutionists spend a lot of time arguing about the intrinsic plausibility of sympatric speciation, and about whether populations become geographically isolated often enough to make allopatric speciation the dominant mode. Nevertheless, sympatric speciation remains appealing for several reasons. It was one of Darwin’s favored modes of speciation in *The Origin*, making it beloved of Darwinophiles. Moreover, adaptationists are enamored of the idea that, during sympatric speciation, natural selection acts *directly* to favor the creation of new reproductively isolated groups. (During allopatric speciation, the appearance of reproductive isolation is an evolutionary accident.)

What evidence is required to make a compelling case for sympatric speciation?

Because of the difficulties of sympatric speciation, proposed cases must be scrutinized carefully; as Carl Sagan said, “extraordinary claims require extraordinary evidence.” (This does not mean, of course, that other modes of speciation require no evidence.) Establishing a compelling case for sympatric speciation requires meeting four conditions. First, the species must be largely or completely sympatric. (While species could have speciated sympatrically and subsequently become allopatric,

this is almost impossible to demonstrate.) Second, the sympatric species must show substantial reproductive isolation, preferably based on genetic differences. Third, the sympatric taxa must be sister species: each other's closest relatives. There is a problem with meeting this criterion, because if there is any hybridization between sympatric taxa, they will become genetically similar, appearing closely related even if they aren't. Fourth, the biogeographic and evolutionary history of the groups must make the existence of an allopatric phase *very unlikely*. This is perhaps the most difficult requirement, for it requires assurance that incipient species were never geographically isolated — even for a relatively short time — over the thousands or millions of years required to attain reproductive isolation.

The best way to find cases of sympatric speciation is to search for closely related species in habitat 'islands' such as isolated lakes or small, remote oceanic islands. If these islands contain endemic sister species of mobile organisms, it is likely that those species evolved without physical isolation.

Are there any really convincing examples of sympatric speciation?

Because of the difficulty of establishing the above requirements, there are no absolutely airtight examples of sympatric speciation. But there are at least a few cases in which sympatric speciation seems extremely likely. One involves several species of cichlid fish in two very small Nicaraguan volcanic-crater lakes, with all the cichlids in each lake being closely related descendants of a single common ancestor. It's unlikely that fish in these lakes could ever have been geographically isolated because the lakes are extremely small, conical, and uniform. Other small glacial lakes in Iceland also harbor closely related fish species likely to have speciated sympatrically.

On tiny Lord Howe Island in the Pacific, there are two sister species of palm tree that are probably the results of speciation

on the island. Two host races of the tephritid fruit fly *Rhagoletis pomonella* live sympatrically on hawthorn and apple fruits, with the apple race having formed within the past 150 years. Although these races are not full species, they have been carefully studied and we know that a substantial amount of reproductive isolation evolved in sympatry. In some cases a single species of host harbors two sister species of host-specific parasites (this has been found in fish flukes). Because a host can be considered as an island for the parasite, this might imply sympatric speciation within a host. This conclusion is complicated, however, by the possibility that new species of parasite could actually form allopatrically in geographically isolated populations of the host, and then doubly infect the host when the host populations re-establish contact. Indigobirds, which are nest parasites, have colonized new host species in sympatry, and such host invasions lead to reproductively isolated lineages because male and female parasites behaviorally imprint on the hosts. (This is a form of nongenetic speciation!)

Finally, polyploidy in plants is a type of sympatric speciation in which two sympatric species having different chromosome numbers or morphologies form a hybrid, and that hybrid produces offspring with a doubled number of chromosomes (one full genome from each parental species). This yields a new lineage that is reproductively isolated from both ancestral species. Polyploid speciation is quite common in plants, perhaps accounting for up to 4% of new angiosperm species.

So even if there are some cases of sympatric speciation, how important is it?

Finding examples of sympatric speciation does not tell us how common it is in nature. It could be relatively uncommon: for although evolutionists concentrate on groups in which sympatric speciation is most likely, there are still only a handful of plausible examples. Or, it could be common, but the conditions under which we can actually detect it are extremely rare. One

way to settle the problem is to thoroughly survey the flora and fauna of small, isolated habitat islands, scrutinizing many taxa for the presence of sister species that might have formed sympatrically. Unfortunately, there are only two such studies that have been reported, one on birds living on isolated oceanic islands and the other on *Anolis* lizards on Caribbean islands. Both studies show that sister species do *not* form on small islands, so that sympatric speciation seems rare or nonexistent in these groups. But we need more such studies, particularly of insects, plants, and fish. At present, then, although further cases of sympatric speciation will certainly be uncovered, it will probably not be nearly as common as other forms of geographic speciation. The process will still be of interest, however, in demonstrating how natural selection and, in particular, ecological adaptation can translate directly into reproductive isolation.

Where can I find out more about sympatric speciation?

- Berlacher, S.H., and Feder, J.L. (2002). Sympatric speciation in phytophagous insects: moving beyond controversy? *Ann. Rev. Entomol.* 47, 773–815.
- Coyne, J.A., and Orr, H.A. (2004). Speciation. (Sinauer Associates, Sunderland, MA).
- Coyne, J.A., and Price, T.D. (2000). Little evidence for sympatric speciation in island birds. *Evolution* 54, 2166–2171.
- Gavrilets, S. (2004). Fitness Landscapes and the Origin of Species. Princeton University Press Monographs in Population Biology, Princeton.
- Losos, J.B., and Schluter, D. (2000). Analysis of an evolutionary species-area relationship. *Nature* 408, 847–850.
- Otto, S.P., and Whitton, J. (2000). Polyploid incidence and evolution. *Annu. Rev. Genetics* 34, 401–437.
- Savolainen, V., Anstett, M.-C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V., Powell, M.P., Springate, D., Salamin, N., and Baker, W.J. (2006). Sympatric speciation in palms on an oceanic island. *Nature* 441, 210–213.
- Simková, A., Morand, S., Jobet, E., Gelnar, M., and Verneau, O. (2004). Molecular phylogeny of congeneric monogenean parasites (*Dactylogyrus*): A case of intrahost speciation. *Evolution* 58, 1001–1018.
- Schliewen, U.K., Tautz, D., and Pääbo, S. (1994). Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368, 629–632.
- Sorenson, M.D., Sefc, K.M., and Payne, R.B. (2003). Speciation by host switch in brood parasitic indigobirds. *Nature* 424, 928–931.

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