

# Speciation in the apple maggot fly: a blend of vintages?

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**The importance of speciation without the complete geographical separation of diverging populations (sympatric speciation) has become increasingly accepted. One of the textbook examples of recent speciation in sympatry is the apple maggot fly *Rhagoletis pomonella*, in which genetically differentiated host races feed on either hawthorn or apple. Three recent articles by Feder and collaborators show that the history of these host races is more complicated than was previously realized. Genes that differentiate races of flies that feed on either apple or hawthorn are located in chromosomal rearrangements. This variation forms a latitudinal cline that must have been established long before apples were available as hosts. Furthermore, there is also new evidence for the very recent evolution of a derived preference for volatile chemicals that are typical of apple fruits among apple-feeding flies. These results show that adaptation to apple populations has involved both the sorting of ancestral adaptive variation and the selection of novel mutations.**

Dobzhansky is reported to have said that a belief in SYMPATRIC SPECIATION (see Glossary) is 'like the measles; everyone gets it and we all get over it' [1]. If this is the case, then there seems to have been a recent epidemic, with ADAPTIVE RADIATION and sympatric speciation increasingly seen as major forces in the generation of biodiversity. In a sense, sympatric speciation is the most extreme form of adaptive speciation, in that natural selection alone is responsible for the establishment of barriers to gene flow from an initial condition of random mating. This contrasts with the widely accepted view that speciation requires some form of geographical barrier (ALLOPATRIC SPECIATION). The textbook example of sympatric speciation is *Rhagoletis pomonella*, the apple maggot fly. Populations of this tephritid fly in northeastern USA switched from the ancestral host, hawthorn, to feed on introduced apples sometime during the mid-19th century. As apples and hawthorn commonly grow together within the 'cruising distance' of a fly, this is most likely to have been a sympatric adaptive switch onto a new host. Reproductive isolation between host races is due, largely, to host choice, because flies mate on their hosts with individuals that have made a similar choice [2].

## Chromosomal rearrangements and speciation

Three recent papers add some novel twists to the *Rhagoletis* story [3–5]. First, the six allozyme loci that have long been known to be differentiated between apple and hawthorn races of *Rhagoletis* [6] are all located in chromosomal rearrangements [4]. Unfortunately, owing to practical limitations, the exact pattern of these rearrangements remains unknown. Only small families generated from single pair crosses can be reared for genetic mapping, giving limited linkage information per family. In addition, cytogenetic techniques for studying chromosome-banding patterns are poorly developed in this species. Nonetheless, it is estimated that as much as half of the genome of *Rhagoletis* is included in these three chromosomal rearrangements.

This highlights what might be a novel and unexpected line of support for sympatric and/or PARAPATRIC SPECIATION in several taxa. Recent studies of sunflowers *Helianthus* spp. and fruit flies *Drosophila* spp. have shown that genic differences between species are found disproportionately in inversions [7,8]. The most probable reason for these observations is that such chromosomal rearrangements reduce RECOMBINATION between diverging genomes, making the accumulation of genetic differences more probable within such rearrangements (Box 1). By contrast, there appears to be no reason why populations diverging in allopatry should accumulate differentiation, adaptive or otherwise, in chromosomal rearrangements. In sunflowers and fruit flies, therefore, these observations support a model of speciation in which

## Glossary

**Allopatric speciation:** speciation caused by complete geographic separation of diverging populations.

**Adaptive radiation:** the divergence and speciation of a community of organisms driven by adaptation and the partitioning of ecological opportunities between species.

**Linkage disequilibrium:** an association between alleles within a population that differs from that expected under random mating.

**Parapatric speciation:** the evolution of a new species between geographically abutting and hybridizing populations. Also sometimes termed 'ecotonal speciation', where adaptation to an ecological cline is implicated as the cause of divergence.

**Recombination:** the process by which offspring derive combinations of alleles different from those present in either parent. This can occur by a number of processes, including crossing over and gene conversion.

**Sympatric speciation:** the evolution of a new species from the initial state of a single randomly mating population, without any geographic separation of diverging populations.

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there has been gene flow between incipient species for a considerable period of time during divergence (i.e. 'parapatric' or 'sympatric' speciation).

Unfortunately however, it is still premature to include *Rhagoletis* as an example of this phenomenon. Although all the known genetic differences between host races are found in inversions, any scan of loci for differentiation is inherently biased towards detecting differences within inverted regions. This is because the reduction in recombination within these chromosome regions between races means that many genes are in complete LINKAGE DISEQUILIBRIUM (i.e. new mutations within this region remain strongly associated with each other during their history; Box 1). As well as enabling adaptive differences to be maintained under conditions of gene flow, this also increases the chromosomal area over which neutral differentiation (as detected by a screen of allozyme loci) is generated by divergent selection. By contrast, if other loci involved in host adaptation lie outside these inversions, they are likely to have remained undetected because recombination will reduce the size of the region in which

marker loci are in strong association with the selected gene. To resolve this problem and to determine how much reproductive isolation is due to genes in inversions, an unbiased search for loci involved in reproductive isolation is needed, for example through an analysis of quantitative trait loci for host choice.

### The geographical origin of chromosomal rearrangements

However, whereas the association of species differences with inversions provides a new line of support for speciation under conditions of ongoing gene flow, it also seems to challenge the traditional *Rhagoletis* story. Genetic differences between apple and hawthorn flies must predate the introduction of apples to the USA in the 19th century, because extensive chromosomal rearrangements are very unlikely to have arisen over such a short time. To confirm this, Feder *et al.* studied the genealogical history of the three inversions [3]. The three gene trees show a strikingly concordant pattern. Inversion haplotypes found at high frequency in apple populations are

#### Box 1. Why do chromosomal rearrangements assist local adaptation?

When chromosomal rearrangements, such as inversions, segregate in a population, they greatly reduce recombination between alleles within the affected region. This is because crossing over during meiosis is prevented where chromosomal regions are non-homologous between chromosome pairs (recombination can still occur through the much less frequent process of gene conversion). This reduction in the recombination rate can favour the accumulation of adaptations to alternate habitats. Imagine that 'A' is an allele that increases the fitness of individuals on apple hosts relative to 'a', and is located in a chromosomal inversion (in Figure 1, the inversion is shown as a red bar in the hawthorn population and a grey bar in the apple population, with the surrounding recombining chromosomal regions shown in blue). A subsequent mutation that also increases fitness on apples is more likely to go to fixation at locus B, within the inversion, than at locus C that lies outside the inversion. In both instances, hybridization between apple and hawthorn populations can produce intermediate F1 individuals, AaBb, or AaCc that are not well adapted to either host population. However, when two F1 individuals mate (i.e. an F2 cross), if there is no recombination then 50% of the offspring will be well adapted parental gene combinations (Figure 1a, i.e. aabb and AABB), but, with recombination, this proportion will be reduced to as little as 12.5%, because of the production of maladapted recombinant genotypes (Figure 1b). Hence, the cost of hybridization is higher for alleles located outside the inversion, reducing their chance of spread. Therefore, clustering of alleles for adaptation to alternate habitats within inversions is favoured where hybridization occurs and alleles need to be inherited together to increase fitness on some hosts. The observation of such clustering might therefore provide evidence to support speciation under conditions of pervasive gene flow (parapatric or sympatric) [10].

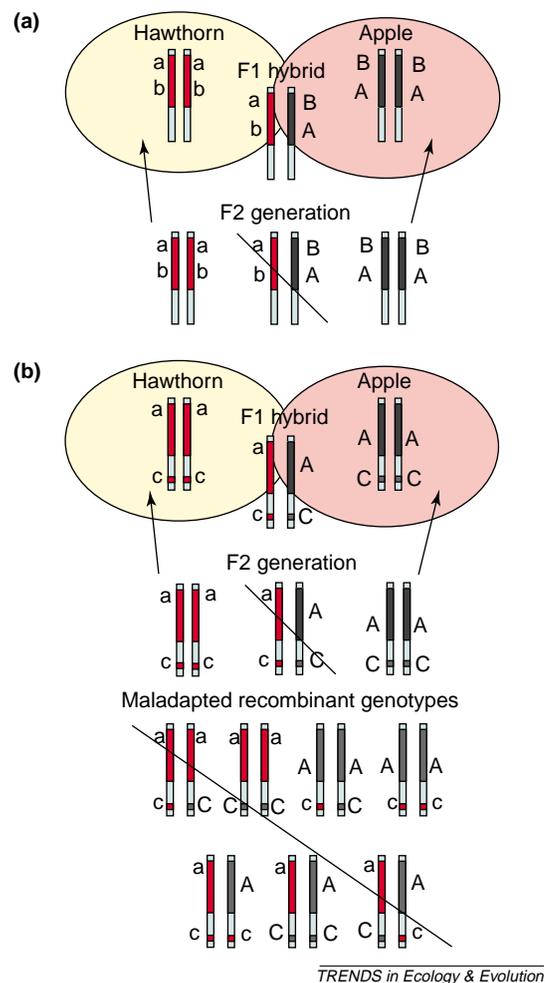


Figure 1.

more closely related to those from Mexico and the southern US than to those common in sympatric northern USA hawthorn flies. The implication, therefore, is that at least some of the genetic variation that gave rise to the apple flies was derived from the spread of genes already established in ancestral southern USA hawthorn populations.

Two lines of argument support this as a case of pre-existing adaptive variation rather than the generation of a chance association between inversions and novel apple adaptations. First, there is no evidence for reduced levels of variation within apple-specific inversions that might indicate very recent selective sweeps. Second, for an apple maggot fly, living in Texas is a bit like eating apples. The most important known adaptive differences between apple and hawthorn flies relate to diapause. The deeper diapause that is characteristic of hawthorn populations from southerly latitudes is similar to that known to be important in early-fruited apple populations. Both involve warmer autumn days immediately following pupation compared with the northern hawthorn flies, which go into diapause when the weather is already much colder [3].

The overall conclusion, therefore, is that at least some of the genetic variability that enabled the sympatric host switch to apples in the 19th century was derived from pre-existing geographical variation. Feder *et al.* [3] use a simulation analysis to test for concordance between nodes on the three nuclear and mtDNA trees, and conclude that the node coinciding with the north–south split is the most concordant among the trees and dates to  $\approx 1.5$  million years before present. A shared time of divergence among genes, such as that observed here, is often used as evidence for a vicariance event leading to divergence across the genome [3]. However, it is equally compatible with an environmental shift that enabled ancestral populations to move south and adapt to lower latitudes, without requiring complete geographical separation. Whatever the specific biogeographical details, it is clear that the adaptive differences between apple and hawthorn races were derived from a pre-existing geographical cline established in either parapatry or allopatry.

Interestingly, another well studied example of adaptive speciation, the Canadian lake stickleback *Gasterosteus aculeatus*, also shows evidence for an initial phase involving geographical separation, because the locally adapted benthic and limnetic forms appear to have resulted from double invasions from marine systems [9]. Therefore, it seems that the initial allelic disequilibrium established during geographical separation could enhance the chances of character displacement and speciation in sympatry, by enabling clusters of genes to spread together under selection. The spread of many alleles simultaneously, without the short-term cost of recombination, might be important when adaptation to rapidly changing conditions is required, or during adaptive radiation when organisms move into novel habitats.

### Sympatric or allopatric?

However, celebration among those who find sympatric speciation implausible would be premature. A major

source of reproductive isolation between *Rhagoletis* host races is due to host-specific mating. So, even if some of the genetic variation necessary for the switch to apples originally arose in allopatry, it was the sympatric colonization of a new niche and increase in frequency of ‘southern’ haplotypes within that niche that led to reproductive isolation. Host associations lead to pleiotropic mate choice, which reduce the rate of recombination and enable further divergence of the different inversion haplotypes in sympatry. Therefore, although allopatric origins might have provided the genetic variability necessary, the sympatric switch onto a novel host was the trigger for speciation. Furthermore, in addition to the sorting of pre-existing variation, the level of reproductive isolation observed today results, at least in part, from novel adaptations related to host discrimination that have arisen over the past 200 years. In another recent paper [5], it was shown that, in both field and wind-tunnel experiments, apple flies are more attracted to volatile chemicals that are typical of apples than they are to those of hawthorn fruit. Hawthorn flies and the closely related flowering dogwood fly, *Rhagoletis* sp. nov., do not show such a preference for apple volatiles, implying that the preference has recently evolved in apple flies. The taxa that we see today have therefore resulted, in part, from the sorting of pre-existing ancestral variation, followed by the rapid evolution and substitution of entirely novel host-choice adaptations.

Nature is complicated, and textbook examples often turn out to be more convoluted than we might like. In this case, the biogeographical history of a whole species complex has helped to illuminate a sympatric host shift. One of the most intractable of evolutionary questions concerns whether adaptation primarily involves the selection of pre-existing genetic variation, or has to wait for novel mutations to arise in the population exposed to new selection pressures. In the case of the *Rhagoletis* host shift, it seems that the former has played an important role. A deeper understanding of examples such as *Rhagoletis* will enable studies of speciation to move away from the traditional and increasingly sterile discussion of sympatric and/or allopatric modes of speciation into more fruitful consideration of where genetic variation for adaptive radiation comes from, what limits the rate of allelic substitution, and the nature of the constraints placed on evolution by the structure of gene and developmental networks.

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## Letters

# What is right with ‘teaching the controversy’?

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In an important recent Opinion article in *TREE* [1], Eugenie Scott and Glenn Branch propose five criteria for evaluating whether it is appropriate to teach a controversy in a public school science class. They argue that anti-evolutionary alternatives to the standard science account of organic evolution fail on most of the five criteria and, therefore, should not be discussed within the framework of a science course.

I propose a sixth criterion: the controversy should be taught if it clarifies the demarcation between science and other ways of knowing about nature. Most introductory biology texts (e.g. [2–4]) begin with a chapter that reviews both the foundational assumptions about nature that underlie science (e.g. natural phenomena have natural causes, natural ‘laws’ operate everywhere and for all time), and the ethical ideals that the scientific community recognizes as being essential for scientific knowledge to progress (e.g. detailed public reporting of scientific research so that peers can accurately evaluate and replicate it, all accepted scientific claims are provisional and therefore might be revised or rejected upon further review). US national science education standards direct high-school science teachers to cover the assumptions and ethics of science [5].

The most popular antievolutionary alternatives to the standard scientific account, young earth creationism and ‘intelligent design theory’, reject or weaken several of the foundational assumptions and ethical ideals of science. For example, young earth ‘creation science’ adds an additional assumption that supercedes all others: the Bible is inerrant and literally true, therefore scientific claims about nature can only be valid if they do not violate this assumption. Because so many forms of material evidence indicate that the Earth is far older than 6000 years, creationists are forced to infer that natural processes were radically different in the past compared with what is observed

today; for example, radioactive decay rates were far more rapid a few thousand years ago, making the Earth seem older than it really is\*.

I teach an introductory biology class to first-year college students who are not specializing in science. They are not far removed from the high-school classroom, and their science literacy is generally rudimentary and rife with the fundamental scientific misconceptions reviewed in [6]. After an introduction to the beliefs and practices of science, I spend much of my course focusing on Darwin, Mendel, the modern synthesis, and the history of life on Earth. I then tackle the issue of antievolutionary alternatives to the standard scientific account; I provide an overview of the basic claims of young earth creationism and intelligent design theory, and then have students evaluate them in relation to the foundational assumptions and ethical ideals of science. I provide my opinion about why these antievolutionary theories are merely pseudoscientific alternatives to the standard scientific account, followed by a discussion among the students on whether these popular antievolutionary alternatives can truly be categorized as science.

It has been my experience that many students are skeptical of professorial dogma, especially on a subject of popular controversy, such as organic evolution, and consider it disingenuous when a teacher avoids presenting popularly held beliefs that differ from the instructor’s own. To ignore antievolutionary theories in the science classroom because they are not accepted science beggars the question what, indeed, is accepted science? Examining antievolutionary theories in relation to the assumptions and ideals of standard accepted science can help to clarify on what ethical and epistemological grounds most scientists come to vehemently reject antievolutionary claims as coequal rivals to the standard evolutionary account. When I assess students, I find that most, including committed

\* Chafin E.F. (2003) Accelerated decay: Theoretical Models. *Proceedings of the International Conference on Creationism 2003* (<http://www.icr.org/research>)