

## Book Review

## Speciation: Darwin revisited

### Frogs, Flies, and Dandelions. The Making of Species

by Menno Schilthuizen. Oxford University Press, 2001. £17.95 hbk (245 pages)  
ISBN 0 19 850393 8

A good, popular science book is hard to find. Even when a subject has a wide appeal (as the origin of biodiversity surely has), only rarely can an author find the right balance between accuracy and simplicity.

Fortunately, Schilthuizen has done an excellent job on this book. Strange though it might sound, I can recommend his book to almost everyone – from a specialist in SPECIATION (see Glossary), to a biochemist, to a curious astrophysicist, and to any lay, scientifically literate person. On the one hand, the book is remarkably up-to-date and is saturated with facts and ideas. More than once I forgot that I was reading a popular book and felt an urge to dispute various fine points made by the author. On the other hand the book is both easy and fun to read.

The coverage of species and speciation is comprehensive. The book begins with discussion of the nature of species, and then considers ALLOPATRIC SPECIATION,

possible roles of random GENETIC DRIFT and SEXUAL SELECTION, instant speciation, and different aspects of SYMPATRIC SPECIATION. Theoretical ideas are explained verbally (although pictures of adaptive surfaces would have been helpful), and recent data are presented with fascinating biological details.



Better still, the book sets straight the record distorted by the so-called 'Modern Synthesis'. As anybody who bothers to read '*The Origin of Species*' (Chapter 4) can see, Darwin treated speciation in depth and believed that it is driven by natural selection caused by competition between sympatric organisms. However, in the middle of the last century it somehow became widely accepted (a) that

Darwin did not understand the origin of species; (b) that sympatric speciation does not happen; and (c) that the driving force behind speciation is genetic drift, because the key stage of the process is counteradaptive. One might think that such abuse should be reserved for those Russians who commit all their thoughts to the pages of *Siberian Ecological Journal* (<http://www-psb.adsbras.nsc.ru/secjw.htm>) – an interesting journal, if only you could read it.

Fortunately, we are witnessing the darwinian restoration. Origin of species, after all, is by means of natural selection, and sympatric speciation, as well as theoretically trivial allopatric speciation, does happen. Finally, we could instead concentrate on real issues – what are 'speciation genes'? What is the contribution of different modes of speciation to the diversity within particular taxa? What modes of selection drive sympatric speciation? Even these cutting-edge issues are covered by Schilthuizen, and his book provides an idea of how speciation research will develop in the near future.

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## Glossary

### Speciation Glossary

**Adaptive radiation:** the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage.

**Allopatric speciation:** the origin of two or more species resulting from divergent evolution of populations that are geographically isolated from one another.

**Allopatry:** geographical separation, such that members of two or more populations fail to encounter one another.

**Anagenesis:** evolution within a lineage, usually expressed by morphological change, but not associated with a splitting event.

**Assortative mating:** Non-random choice of a mate, either directly through the evaluation of some attribute, or indirectly through habitat choice (for taxa that mate within their habitat)

**Beavis effect:** systematic overestimation of true quantitative trait locus effects. The Beavis effect is most severe when F2 or backcross sample sizes are small.

**Biometric (estimation of gene number):** an approach to estimating the minimum number of genes underlying a trait difference that relies only on phenotypic data.

**Bottleneck:** a short-term drastic reduction in population size, which can occur either through much-reduced survival within a population or accompanying colonization of a new habitat.

**By-product mechanism:** a mechanism of speciation in which premating and/or postmating reproductive isolation evolves incidentally as a consequence of evolution of other traits. Reproductive isolation is not directly favored by selection, in contrast to reinforcement.

**Centromere:** the constricted region of a chromosome to which spindle fibers attach during division.

**Chromosomal fission:** breakage of chromosome segments.

**Chromosomal fusion:** reunion of previously independent chromosome segments.

**Chronospecies:** a species that is part of the continuum of a lineage documented in the fossil record, distinguished from the chronospecies below and above by the accumulation of sufficient morphological change over time.

**Clade:** a monophyletic group of organisms.

**Cladistics:** method of drawing trees of organismal relationships founded on shared derived characters.

**Cladogenesis:** the splitting of a species lineage.

**Disruptive selection:** natural selection within a single population towards two different (usually extreme) phenotypes, for example, when large or small individuals have an advantage over those of intermediate size.

**Divergent selection:** natural selection in different directions within each of several populations, for example, when large size is favored in one population, whereas small size is favored in another. Intermediates are never favored.

Diversification rate: the net rate of increase in species numbers within a group, equal to the speciation rate minus the extinction rate over a given period.

Dobzhansky–Muller incompatibilities: epistatic incompatibilities that appear in hybrids as a result of interaction between alleles that did not lower fitness when they were substituted within the diverging lineages.

Ecological mechanism of reduced hybrid fitness: the reduced hybrid fitness resulting from direct natural selection against intermediate phenotypes, and whose presence depends on niche characteristics of environment in which hybrids are tested.

Ecological speciation: the evolution of reproductive isolation caused ultimately by divergent natural selection on traits between populations (or disruptive selection between phenotypes of a single population) in different environments (including use of different resources).

Ecophenotypic change: non-evolutionary change in the morphology, or other characters, of an organism, usually induced by environmental pressures.

Ecotype: an ecologically and phenotypically distinct group of individuals. Members of an ecotype might belong to the same species or to different species.

Extrinsic incompatibilities: forms of reproductive isolation (usually sterility or inviability of hybrids) whose presence or intensity depends on the particular environment in which the hybrids are tested.

Genealogical: pertaining to the history of descent of genes, often within a single species.

Genetic drift: stochastic fluctuations produced by sampling in finite populations.

Haldane's rule: the observation that, if hybrids of only one sex are sterile or inviable in a species cross, that sex is nearly always the one having heterogametic sex chromosomes.

Heterochromatin: densely staining condensed chromosomal regions, believed for the most part to be genetically inert.

Incipient species: two or more diverged populations that are substantially, but not completely, reproductively isolated.

Internal nodes: branching points on a phylogenetic tree that reflect past speciation events leading to living species.

Intrinsic incompatibilities: forms of reproductive isolation that are relatively independent of the environment in which hybrids are tested. Such incompatibilities usually reflect developmental abnormalities produced by deleterious epistatic interactions between alleles from different species.

Inversion: a chromosomal mutation involving the removal of a chromosome segment, its rotation through 180°, and its reinsertion in the same location.

Karyotype: the chromosome complement of an organism.

Large X effect: the observation that, in genetic analyses of hybrid sterility and incompatibility, the X chromosome tends to have the largest effect among all the chromosomes, especially when examined in hybrids with heterogametic sex chromosomes.

Lineage: a chronological sequence of populations with ancestor–descendant relationships.

Linkage disequilibrium: non-random associations between alleles at different loci.

Linkage: physical proximity of genes on the same chromosome that reduces the frequency of recombination between them.

Meiotic drive: a distortion in the transmission ratio of a particular gene or chromosomal rearrangement at meiosis.

Mendelize: a trait difference between two species or populations is said to mendelize if the genetic basis of the difference is sufficiently simple that the trait segregates in simple mendelian ratios in F2 or backcross hybrids.

Monandrous mating system: a female mates with

only one male during the breeding season.

Monophyletic: containing all the descendants of a hypothetical common ancestor.

Morphological species concept: a species is defined by being sufficiently morphologically distinct from all others. The definition can include multivariate tests of the statistical distance between species centroids in relation to intraspecific variation about the centroids.

Mosaic hybrid zone: a region with a patchy distribution of parental and hybrid genotypes, as opposed to a smooth and continuous geographical transition from one parental species to the other through an area of hybridization.

Neospecies: a newly derived species.

Network: diagram of relationships allowing lateral connections among groups.

Neutral alleles: allelic variants at a locus that have no effect on the fitness of the bearer.

One-allele mate choice: substitution of a single 'assortative mating' allele that causes all individuals, in any environment, to mate assortatively. A biologically plausible example would be if all individuals mate where they were raised. This causes assortative mating because individuals subjected to the same forces of selection become mates.

Parallel speciation: parallel evolution of traits underlying reproductive isolation in independent populations evolving along similar environmental gradients.

Parapatric speciation: the evolution of substantial reproductive isolation between spatially adjacent populations that have limited gene exchange.

Parapatric: the abutting of geographical ranges of populations, such that only the members of populations at the contact edges of geographical ranges encounter one another.

Paraphyletic: containing the descendants of a common ancestor that retain shared primitive characters, but omitting descendants that have lost those characters.

Pericentric inversion: the inversion of chromosomal material that includes the centromere.

Phenotypic divergence: divergence of trait means between two or more populations (or subpopulations).

Phyletic gradualism: the view that species evolve by gradual lineage evolution (anagenesis) and splitting (speciation) as a subsidiary process.

Phylogenetic tree: an estimate of the true phylogeny, for example as might be reconstructed from species characters such as molecular data. Often shortened to tree.

Phylogenetics: pertaining to evolutionary relationships among organisms, usually at or above the level of species.

Phylogeny: the evolutionary relationships among a group of organisms.

Phylogeography: analysis of biogeographic patterns in light of phylogeny, often at the level of populations within named species.

Pleiotropy: multiple effects of alleles on more than one character. Pleiotropy leads to correlated responses to selection because allele frequency change caused by selection alters the value of all of the traits affected by a pleiotropic allele.

Polyandrous mating system: a female mates with multiple males during the breeding season.

Postzygotic isolation: reproductive isolation that occurs after fertilization, such as hybrid sterility and hybrid inviability.

Prezygotic isolation: reproductive isolation that occurs before fertilization. Includes species differences in traits such as sexual behaviour, habitat preference, seasonal breeding (all premating), and gametic compatibility (postmating but prezygotic).

Punctuated equilibria: the view that speciation occurs relatively rapidly, and that virtually all evolution happens at speciation (cladogenesis), with

long intervening phases of stasis of lineages.

Punctuation: a rapid speciation event, forming part of the model of evolution by punctuated equilibria.

Quantitative trait locus (QTL): a chromosome region having a statistically significant effect on a phenotypic difference between two lines, populations, or species.

Quantitative trait locus mapping: use of a genetic linkage map to locate chromosomal segments that influence phenotypic traits of interest.

Race: used here as a synonym for incipient species, without the requirement that two races be geographically separated.

Reinforcement: the adaptive strengthening of prezygotic isolating mechanisms in a zone of secondary contact between two distinct taxa that have previously evolved some postzygotic isolation. In this process, natural selection reduces gene flow between the taxa because hybridization is deleterious.

Reproductive character displacement: the evolution of increased differences between two established species in sympatry, which might result from the production of hybrids that are less fit or from efforts wasted on unsuccessful interspecific mating interactions.

Reproductive isolation: absence (or severe restriction) of gene flow between populations whose members are in contact with one another.

Secondary contact: the co-occurrence in one area of two taxa that were previously geographically isolated and had accumulated some genetic divergence.

Secondary sexual traits: sex specific traits used in mating competition that are not directly involved in reproduction. Some examples include the colourful feathers of many bird species, antlers in several ungulates, and songs of many insects, frogs and birds.

Sexual selection: differential reproductive success resulting from competition for fertilization.

Competition for fertilization occurs through direct competition between members of the same sex or through the attraction of one sex to the other.

Speciation: the establishment of reproductive isolation between two or more previously interbreeding populations.

Species selection: the hypothetical process of sorting of species, which might involve selection for survival of those that possess particular irreducible, emergent, species-level characteristics.

Stasis: long episodes of no net morphological change in a species lineage.

Step cline: a cline with a large or steep step.

Sympatric speciation: speciation occurring within a single geographical area, so that reproductive isolation arises between individuals that always have the opportunity to interbreed.

Sympatry: absence of geographical separation, such that all individuals have the same chance of meeting each other.

Taxonomic: pertaining to the classification of organisms, not necessarily based on their evolutionary relationships.

Tension zone: a hybrid zone maintained primarily by selection against hybrids or rare genotypes, rather than by adaptation of alternative alleles to alternative environments.

Translocation: the exchange of chromosomal segments between nonhomologous chromosomes.

Two-allele mate choice: different alleles cause mating in each of two environments. This can only lead to assortative mating when mating alleles are in linkage disequilibrium with alleles under disruptive selection.

Unbalanced gametes: gametes that carry chromosomal duplications or deficiencies.

Underdominant (selection): Selection against heterozygotes, as might occur with chromosome rearrangements.

Underdominant mutation: a mutation that causes reduced fitness when heterozygous.