Síntesi evolutiva moderna

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Diverses idees importants sobre l'evolució es van unir en la genètica de poblacions de principis del segle XX per formar la síntesi moderna, incloent la variació genètica, la selecció natural i l'herència de partícules (mendeliana). [1] Això va posar fi a l'eclipsi del darwinisme i va suplantar una varietat de teories no darwinianes de l'evolució.

Forma part d'una sèrie sobre

Biologia evolutiva

Els pinsans de Darwin, de John Gould

Esquema
principal
de la introducció
de l'índex

Historial
d'evidències del
glossari

show
Processos i resultats

show
Història natural

show
Història de la teoria evolutiva

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La síntesi moderna és la síntesi de principis del segle XX que concilia la teoria de l'evolució de Charles Darwin, també coneguda com la bunda i les idees de Gregor Mendel sobre l'herència en un marc matemàtic conjunt. Julian Huxley va encunyar el terme en el seu llibre de 1942, Evolution: The Modern Synthesis.

Les idees del segle XIX sobre la selecció natural i la genètica mendeliana es van elaborar juntament amb la genètica de poblacions, a principis del segle XX. La síntesi moderna també va abordar la relació entre els canvis a gran escala de macroevolució observats pels paleontòlegs i la microevolució a petita escala de les poblacions locals d'organismes vius. La síntesi va ser definida de manera diferent pels seus fundadors, amb Ernst Mayr el 1959, G. Ledyard Stebbins el 1966 i Theodosius Dobzhansky el 1974 oferint diferents nombres de postulats bàsics, encara que tots inclouen la selecció natural, treballant en la variació hereditària subministrada per mutació. Altres figures importants en la síntesi van ser E.B. Ford, Bernhard Rensch, Ivan Schmalhausen i George Gaylord Simpson. Un dels primers esdeveniments en la síntesi moderna va ser l'article de R. A. Fisher de 1918 sobre genètica matemàtica de poblacions, però William Bateson, i per separat Udny Yule, ja començaven a mostrar com la genètica mendeliana podia funcionar en l'evolució el 1902.

Van seguir diferents síntesis, acompanyant la ruptura gradual de la síntesi de principis del segle XX, incloent-hi el comportament social en la sociobiologia d'E. O. Wilson el 1975, la integració de la biologia evolutiva del desenvolupament de l'embriologia amb la genètica i l'evolució, a partir de 1977, i la proposta de Massimo Pigliucci i Gerd B. Müller de síntesi evolutiva estesa. del 2007. Segons el biòleg evolutiu Eugene Koonin el 2009, la síntesi moderna serà substituïda per una síntesi "postmoderna" que inclourà canvis revolucionaris en la biologia molecular, l'estudi dels procariotes i l'arbre resultant de la vida i la genòmica. [3]

Contingut

Desenvolupaments previs a la síntesi

Teoria de la pangènesi de Darwin. Cada part del cos emet petites gemmules que migren a les gònades i contribueixen a la següent generació a través de l'òvul fecundat. Els canvis en el cos durant la vida d'un organisme s'heretarien, com en el lamarckisme.

Més informació: Història del pensament evolutiu

Evolució de Darwin per selecció natural, 1859
Articles principals: Evolució i Selecció natural

El llibre de Charles Darwin de 1859 Sobre l'origen de les espècies va tenir èxit en convèncer la majoria dels biòlegs que l'evolució s'havia produït, però va tenir menys èxit en convèncer-los que la selecció natural era el seu mecanisme principal. Al segle XIX i principis del XX es van discutir com a alternatives les variacions del lamarckisme (herència de les característiques adquirides), l'ortogènesi (evolució progressiva), el saltacionisme (evolució per salts) i el mutacionisme (evolució impulsat per mutacions). [4] Alfred Russel Wallace va advocar per una versió selectiva de l'evolució, i a diferència de Darwin va rebutjar completament el lamarckisme. [5] El 1880, el punt de vista de Wallace va ser etiquetat com a neodarwinisme per Samuel Butler. [6][7]

Blending inheritance, implied by pangenesis, causes the averaging out of every characteristic, which as the engineer Fleeming Jenkin pointed out, would make evolution by natural selection impossible.

Eclipsi del darwinisme, 1880 en endavant

Article principal: L'eclipsi del darwinisme

Des de la dècada de 1880 en endavant, hi havia una creença generalitzada entre els biòlegs que l'evolució darwiniana estava en profunds problemes. Aquest eclipsi de darwinisme (en la frase de Julian Huxley) va sorgir de les debilitats del relat de Darwin, escrit amb una visió incorrecta de l'herència. El mateix Darwin creia en la barreja d'herència, el que implicava que qualsevol nova variació, fins i tot si fos beneficiosa, es debilitaria en un 50% a cada generació, com l'enginyer Fleeming Jenkin va assenyalar correctament el 1868. [8][9] Això al seu torn significava que les petites variacions no sobreviurien prou temps com per ser seleccionades. Per tant, la barreja s'oposaria directament a la selecció natural. A més, Darwin i altres consideraven l'herència lamarckiana de les característiques adquirides completament possible, i la teoria de la pangènesi de Darwin de 1868, amb contribucions a la següent generació (gemmules) que brollaven de totes les parts del cos, en realitat implicava lamarckisme, així com la barreja. [10][11][12]

August Weismann's germ plasm theory. The hereditary material, the germplasm, is confined to the gonads and the gametes. Somatic cells (of the body) develop afresh in each generation from the germplasm.

Plasm germen de Weismann, 1892

Article principal: Plasmó germinal

La idea d'August Weismann, establerta en el seu llibre de 1892 Das Keimplasma: eine Theorie der Vererbung (El plasme germinal: una teoria de l'herència),[13] era que el material hereditari, que ell anomenava el plasm germen, i la resta del cos (el soma) tenien una relació unidireccional: el germen formava plasm el cos, però el cos no va influir en el germen-plasm, excepte indirectament en la seva participació en una població subjecta a selecció natural. Si era correcte, això feia que la pangènesi de Darwin fos errònia, i l'herència lamarckiana impossible. El seu experiment amb ratolins, tallant-se la cua i demostrant que la seva descendència tenia cues normals, va demostrar que l'herència era "dura". [b] Va argumentar fortament i dogmàticament[15] pel darwinisme i contra el lamarckisme, polaritzant les opinions entre altres científics. Això va augmentar el sentiment antidarwinista, contribuint al seu eclipsi. [16][17]

Disputed beginnings

Genetics, mutationism and biometrics, 1900–1918

Main articles: Mutationism and Biostatistics

William Bateson championed Mendelism.

While carrying out breeding experiments to clarify the mechanism of inheritance in 1900, Hugo de Vries and Carl Correns independently rediscovered Gregor Mendel's work. News of this reached William Bateson in England, who reported on the paper during a presentation to the Royal Horticultural Society in May 1900.[18] In Mendelian inheritance, the contributions of each parent retain their integrity rather than blending with the contribution of the other parent. In the case of a cross between two true-breeding varieties such as Mendel's round and wrinkled peas, the first-generation offspring are all alike, in this case, all round. Allowing these to cross, the original characteristics reappear (segregation): about 3/4 of their offspring are round, 1/4 wrinkled. There is a discontinuity between the appearance of the offspring; de Vries coined the term allele for a variant form of an inherited characteristic.[19] This reinforced a major division of thought, already present in the 1890s, between gradualists who followed Darwin, and saltationists such as Bateson.[20]

The two schools were the Mendelians, such as Bateson and de Vries, who favoured mutationism, evolution driven by mutation, based on genes whose alleles segregated discretely like Mendel's peas;[21][22] and the biometric school, led by Karl Pearson and Walter Weldon. The biometricians argued vigorously against mutationism, saying that empirical evidence indicated that variation was continuous in most organisms, not discrete as Mendelism seemed to predict; they wrongly believed that Mendelism inevitably implied evolution in discontinuous jumps.[23][24]

Karl Pearson led the biometric school.

A traditional view is that the biometricians and the Mendelians rejected natural selection and argued for their separate theories for 20 years, the debate only resolved by the development of population genetics.[23][25] A more recent view is that Bateson, de Vries, Thomas Hunt Morgan and Reginald Punnett had by 1918 formed a synthesis of Mendelism and mutationism. The understanding achieved by these geneticists spanned the action of natural selection on alleles (alternative forms of a gene), the Hardy–Weinberg equilibrium, the evolution of continuously-varying traits (like height), and the probability that a new mutation will become fixed. In this view, the early geneticists accepted natural selection but rejected Darwin's non-Mendelian ideas about variation and heredity, and the synthesis began soon after 1900.[26][27] The traditional claim that Mendelians rejected the idea of continuous variation is false; as early as 1902, Bateson and Saunders wrote that "If there were even so few as, say, four or five pairs of possible allelomorphs, the various homo- and heterozygous combinations might, on seriation, give so near an approach to a continuous curve, that the purity of the elements would be unsuspected".[28] Also in 1902, the statistician Udny Yule showed mathematically that given multiple factors, Mendel's theory enabled continuous variation. Yule criticised Bateson's approach as confrontational,[29] but failed to prevent the Mendelians and the biometricians from falling out.[30]

Castle's hooded rats, 1911

Starting in 1906, William Castle carried out a long study of the effect of selection on coat colour in rats. The piebald or hooded pattern was recessive to the grey wild type. He crossed hooded rats with both wild and "Irish" types, and then back-crossed the offspring with pure hooded rats. The dark stripe on the back was bigger. He then tried selecting different groups for bigger or smaller stripes for 5 generations and found that it was possible to change the characteristics way beyond the initial range of variation. This effectively refuted de Vries's claim that continuous variation was caused by the environment and could not be inherited. By 1911 Castle noted that the results could be explained by Darwinian selection on a heritable variation of a sufficient number of Mendelian genes.[31][32][33]

Morgan's fruit flies, 1912

Main article: Thomas Hunt Morgan

Thomas Hunt Morgan began his career in genetics as a saltationist and started out trying to demonstrate that mutations could produce new species in fruit flies. However, the experimental work at his lab with the fruit fly, Drosophila melanogaster[c] demonstrated that rather than creating new species in a single step, mutations increased the supply of genetic variation in the population.[34] By 1912, after years of work on the genetics of fruit flies, Morgan showed that these insects had many small Mendelian factors (discovered as mutant flies) on which Darwinian evolution could work as if the variation was fully continuous. The way was open for geneticists to conclude that Mendelism supported Darwinism. [35]

An obstruction: Woodger's positivism, 1929

Further information: Joseph Henry Woodger

The theoretical biologist and philosopher of biology Joseph Henry Woodger led the introduction of positivism into biology with his 1929 book Biological Principles. He saw a mature science as being characterised by a framework of hypotheses that could be verified by facts established by experiments. He criticised the traditional natural history style of biology, including the study of evolution, as immature science, since it relied on narrative.[36] Woodger set out to play for biology the role of Robert Boyle's 1661 Sceptical Chymist, intending to convert the subject into a formal, unified science, and ultimately, following the Vienna Circle of logical positivists like Otto Neurath and Rudolf Carnap, to reduce biology to physics and chemistry. His efforts stimulated the biologist J. B. S. Haldane to push for the axiomatisation of biology, and by influencing thinkers such as Huxley, helped to bring about the modern synthesis.[36] The positivist climate made natural history unfashionable, and in America, research and university-level teaching on evolution declined almost to nothing by the late 1930s. The Harvard physiologist William John Crozier told his students that evolution was not even a science: "You can't experiment with two million years!"[37]

The tide of opinion turned with the adoption of mathematical modelling and controlled experimentation in population genetics, combining genetics, ecology and evolution in a framework acceptable to positivism.[38]

Elements of the synthesis

Fisher and Haldane's mathematical population genetics, 1918–1930

Main article: A Mathematical Theory of Natural and Artificial Selection

In 1918, R. A. Fisher wrote the paper "The Correlation between Relatives on the Supposition of Mendelian Inheritance,"[39] which showed mathematically how continuous variation could result from a number of discrete genetic loci. In this and subsequent papers culminating in his 1930 book The Genetical Theory of Natural Selection,[40] Fisher showed how Mendelian genetics was consistent with the idea of evolution driven by natural selection.[41][d]

During the 1920s, a series of papers by J. B. S. Haldane applied mathematical analysis to real-world examples of natural selection, such as the evolution of industrial melanism in peppered moths.[41] Haldane established that natural selection could work even faster than Fisher had assumed.[43] Both workers, and others such as Dobzhansky and Wright explicitly intended to bring biology up to the philosophical standard of the physical sciences, making it firmly based in mathematical modelling, its predictions confirmed by experiment. Natural selection, once considered hopelessly unverifiable speculation about history, was becoming predictable, measurable, and testable.[44]

De Beer's embryology, 1930

The traditional view is that developmental biology played little part in the modern synthesis,[45] but in his 1930 book Embryos and Ancestors, the evolutionary embryologist Gavin de Beer anticipated evolutionary developmental biology[46] by showing that evolution could occur by heterochrony,[47] such as in the retention of juvenile features in the adult.[48] This, de Beer argued, could cause apparently sudden changes in the fossil record, since embryos fossilise poorly. As the gaps in the fossil record had been used as an argument against Darwin's gradualist evolution, de Beer's explanation supported the Darwinian position.[49] However, despite de Beer, the modern synthesis largely ignored embryonic development to explain the form of organisms, since population genetics appeared to be an adequate explanation of how forms evolved.[50][51][e]

Wright's adaptive landscape, 1932

Sewall Wright introduced the idea of a fitness landscape with local optima.

Further information: Population genetics § History

The population geneticist Sewall Wright focused on combinations of genes that interacted as complexes, and the effects of inbreeding on small relatively isolated populations, which could be subject to genetic drift. In a 1932 paper, he introduced the concept of an adaptive landscape in which phenomena such as cross breeding and genetic drift in small populations could push them away from adaptive peaks, which would in turn allow natural selection to push them towards new adaptive peaks.[41][53] Wright's model would appeal to field naturalists such as Theodosius Dobzhansky and Ernst Mayr who were becoming aware of the importance of geographical isolation in real world populations.[43] The work of Fisher, Haldane and Wright helped to found the discipline of theoretical population genetics.[54][55][56]

Dobzhansky's evolutionary genetics, 1937

Further information: Genetics and the Origin of Species

Drosophila pseudoobscura, the fruit fly which served as Theodosius Dobzhansky's model organism

Theodosius Dobzhansky, an immigrant from the Soviet Union to the United States, who had been a postdoctoral worker in Morgan's fruit fly lab, was one of the first to apply genetics to natural populations. He worked mostly with Drosophila pseudoobscura. He says pointedly: "Russia has a variety of climates from the Arctic to sub-tropical... Exclusively laboratory workers who neither possess nor wish to have any knowledge of living beings in nature were and are in a minority."[57] Not surprisingly, there were other Russian geneticists with similar ideas, though for some time their work was known to only a few in the West. His 1937 work Genetics and the Origin of Species[58] was a key step in bridging the gap between population geneticists and field naturalists. It presented the conclusions reached by Fisher, Haldane, and especially Wright in their highly mathematical papers in a form that was easily accessible to others.[41][43] Further, Dobzhansky asserted the physicality, and hence the biological reality, of the mechanisms of inheritance: that evolution was based on material genes, arranged in a string on physical hereditary structures, the chromosomes, and linked more or less strongly to each other according to their actual physical distances from each other on the chromosomes. As with Haldane and Fisher, Dobzhansky's "evolutionary genetics"[59] was a genuine science, now unifying cell biology, genetics, and both micro and macroevolution.[44] His work emphasized that real-world populations had far more genetic variability than the early population geneticists had assumed in their models and that genetically distinct sub-populations were important. Dobzhansky argued that natural selection worked to maintain genetic diversity as well as driving change. He was influenced by his exposure in the 1920s to the work of Sergei Chetverikov, who had looked at the role of recessive genes in maintaining a reservoir of genetic variability in a population before his work was shut down by the rise of Lysenkoism in the Soviet Union.[41][43] By 1937, Dobzhansky was able to argue that mutations were the main source of evolutionary changes and variability, along with chromosome rearrangements, effects of genes on their neighbours during development, and polyploidy. Next, genetic drift (he used the term in 1941), selection, migration, and geographical isolation could change gene frequencies. Thirdly, mechanisms like ecological or sexual isolation and hybrid sterility could fix the results of the earlier processes.[60]

Ford's ecological genetics, 1940

E. B. Ford studied polymorphism in the scarlet tiger moth for many years.

Further information: Ecological genetics

E. B. Ford was an experimental naturalist who wanted to test natural selection in nature, virtually inventing the field of ecological genetics.[61] His work on natural selection in wild populations of butterflies and moths was the first to show that predictions made by R. A. Fisher were correct. In 1940, he was the first to describe and define genetic polymorphism, and to predict that human blood group polymorphisms might be maintained in the population by providing some protection against disease.[61][62] His 1949 book Mendelism and Evolution[63] helped to persuade Dobzhansky to change the emphasis in the third edition of his famous textbook Genetics and the Origin of Species from drift to selection.[64]

Schmalhausen's stabilizing selection, 1941

Further information: Stabilizing selection

Ivan Schmalhausen developed the theory of stabilizing selection, the idea that selection can preserve a trait at some value, publishing a paper in Russian titled "Stabilizing selection and its place among factors of evolution" in 1941 and a monograph Factors of Evolution: The Theory of Stabilizing Selection[65] in 1945. He developed it from J. M. Baldwin's 1902 concept that changes induced by the environment will ultimately be replaced by hereditary changes (including the Baldwin effect on behaviour), following that theory's implications to their Darwinian conclusion, and bringing him into conflict with Lysenkoism. Schmalhausen observed that stabilizing selection would remove most variations from the norm, most mutations being harmful.[66][67][68] Dobzhansky called the work "an important missing link in the modern view of evolution".[69]

Huxley's popularising synthesis, 1942

Main article: Evolution: The Modern Synthesis

Julian Huxley presented a serious but popularising version of the theory in his 1942 book Evolution: The Modern Synthesis.

In 1942, Julian Huxley's serious but popularising[70][71] Evolution: The Modern Synthesis[2] introduced a name for the synthesis and intentionally set out to promote a "synthetic point of view" on the evolutionary process. He imagined a wide synthesis of many sciences: genetics, developmental physiology, ecology, systematics, palaeontology, cytology, and mathematical analysis of biology, and assumed that evolution would proceed differently in different groups of organisms according to how their genetic material was organised and their strategies for reproduction, leading to progressive but varying evolutionary trends.[71] His vision was of an "evolutionary humanism",[72] with a system of ethics and a meaningful place for "Man" in the world grounded in a unified theory of evolution which would demonstrate progress leading to humanity at its summit. Natural selection was in his view a "fact of nature capable of verification by observation and experiment", while the "period of synthesis" of the 1920s and 1930s had formed a "more unified science",[72] rivalling physics and enabling the "rebirth of Darwinism".[72]

However, the book was not the research text that it appeared to be. In the view of the philosopher of science Michael Ruse, and in Huxley's own opinion, Huxley was "a generalist, a synthesizer of ideas, rather than a specialist".[70] Ruse observes that Huxley wrote as if he were adding empirical evidence to the mathematical framework established by Fisher and the population geneticists, but that this was not so. Huxley avoided mathematics, for instance not even mentioning Fisher's fundamental theorem of natural selection. Instead, Huxley used a mass of examples to demonstrate that natural selection is powerful and that it works on Mendelian genes. The book was successful in its goal of persuading readers of the reality of evolution, effectively illustrating topics such as island biogeography, speciation, and competition. Huxley further showed that the appearance of long-term orthogenetic trends – predictable directions for evolution – in the fossil record were readily explained as allometric growth (since parts are interconnected). All the same, Huxley did not reject orthogenesis out of hand, but maintained a belief in progress all his life, with Homo sapiens as the endpoint, and he had since 1912 been influenced by the vitalist philosopher Henri Bergson, though in public he maintained an atheistic position on evolution.[70] Huxley's belief in progress within evolution and evolutionary humanism was shared in various forms by Dobzhansky, Mayr, Simpson and Stebbins, all of them writing about "the future of Mankind". Both Huxley and Dobzhansky admired the palaeontologist priest Pierre Teilhard de Chardin, Huxley writing the introduction to Teilhard's 1955 book on orthogenesis, The Phenomenon of Man. This vision required evolution to be seen as the central and guiding principle of biology.[72]

Mayr's allopatric speciation, 1942

Main articles: Systematics and the Origin of Species and Allopatric speciation

Ernst Mayr argued that geographic isolation was needed to provide sufficient reproductive isolation for new species to form.

Ernst Mayr's key contribution to the synthesis was Systematics and the Origin of Species, published in 1942.[73] It asserted the importance of and set out to explain population variation in evolutionary processes including speciation. He analysed in particular the effects of polytypic species, geographic variation, and isolation by geographic and other means.[74] Mayr emphasized the importance of allopatric speciation, where geographically isolated sub-populations diverge so far that reproductive isolation occurs. He was skeptical of the reality of sympatric speciation believing that geographical isolation was a prerequisite for building up intrinsic (reproductive) isolating mechanisms. Mayr also introduced the biological species concept that defined a species as a group of interbreeding or potentially interbreeding populations that were reproductively isolated from all other populations.[41][43][75][76] Before he left Germany for the United States in 1930, Mayr had been influenced by the work of the German biologist Bernhard Rensch, who in the 1920s had analyzed the geographic distribution of polytypic species, paying particular attention to how variations between populations correlated with factors such as differences in climate.[77][78][79]

George Gaylord Simpson argued against the naive view that evolution such as of the horse took place in a "straight-line". He noted that any chosen line is one path in a complex branching tree, natural selection having no imposed direction.

Simpson's palaeontology, 1944

George Gaylord Simpson was responsible for showing that the modern synthesis was compatible with palaeontology in his 1944 book Tempo and Mode in Evolution. Simpson's work was crucial because so many palaeontologists had disagreed, in some cases vigorously, with the idea that natural selection was the main mechanism of evolution. It showed that the trends of linear progression (in for example the evolution of the horse) that earlier palaeontologists had used as support for neo-Lamarckism and orthogenesis did not hold up under careful examination. Instead, the fossil record was consistent with the irregular, branching, and non-directional pattern predicted by the modern synthesis.[41][43]

The Society for the Study of Evolution, 1946

During the war, Mayr edited a series of bulletins of the Committee on Common Problems of Genetics, Paleontology, and Systematics, formed in 1943, reporting on discussions of a "synthetic attack" on the interdisciplinary problems of evolution. In 1946, the committee became the Society for the Study of Evolution, with Mayr, Dobzhansky and Sewall Wright the first of the signatories. Mayr became the editor of its journal, Evolution. From Mayr and Dobzhansky's point of view, suggests the historian of science Betty Smocovitis, Darwinism was reborn, evolutionary biology was legitimised, and genetics and evolution were synthesised into a newly unified science. Everything fitted into the new framework, except "heretics" like Richard Goldschmidt who annoyed Mayr and Dobzhansky by insisting on the possibility of speciation by macromutation, creating "hopeful monsters". The result was "bitter controversy".[52]

Speciation via polyploidy: a diploid cell may fail to separate during meiosis, producing diploid gametes which self-fertilize to produce a fertile tetraploid zygote that cannot interbreed with its parent species.

Stebbins's botany, 1950

The botanist G. Ledyard Stebbins extended the synthesis to encompass botany. He described the important effects on speciation of hybridization and polyploidy in plants in his 1950 book Variation and Evolution in Plants. These permitted evolution to proceed rapidly at times, polyploidy in particular evidently being able to create new species effectively instantaneously.[41][80]

Definitions by the founders

The modern synthesis was defined differently by its various founders, with differing numbers of basic postulates, as shown in the table.

Definitions of the modern synthesis by its founders, as they numbered them

ComponentMayr 1959Stebbins, 1966Dobzhansky, 1974

Mutation
(1) Randomness in all events that produce new genotypes, e.g. mutation [81]
(1) a source of variability, but not of direction[82]
(1) yields genetic raw materials[83]

Recombination
(1) Randomness in recombination, fertilisation[81]
(2) a source of variability, but not of direction[82]

Chromosomal organisation

(3) affects genetic linkage, arranges variation in gene pool[82]

Natural selection
(2) is only direction-giving factor,[81][84] as seen in adaptations to physical and biotic environment[81]
(4) guides changes to gene pool[82]
(2) constructs evolutionary changes from genetic raw materials[83]

Reproductive isolation

(5) limits direction in which selection can guide the population[82]
(3) makes divergence irreversible in sexual organisms[83]

After the synthesis

After the synthesis, evolutionary biology continued to develop with major contributions from workers including W. D. Hamilton,[85] George C. Williams,[86] E. O. Wilson,[87] Edward B. Lewis[88] and others.

Hamilton's inclusive fitness, 1964

Further information: Inclusive fitness and Kin selection

In 1964, W. D. Hamilton published two papers on "The Genetical Evolution of Social Behaviour". These defined inclusive fitness as the number of offspring equivalents an individual rears, rescues or otherwise supports through its behaviour. This was contrasted with personal reproductive fitness, the number of offspring that the individual directly begets. Hamilton, and others such as John Maynard Smith, argued that a gene's success consisted in maximising the number of copies of itself, either by begetting them or by indirectly encouraging begetting by related individuals who shared the gene, the theory of kin selection.[85][89]

Williams's gene-centred evolution, 1966

Further information: Gene-centered view of evolution and Adaptation and Natural Selection

In 1966, George C. Williams published Adaptation and Natural Selection, outlined a gene-centred view of evolution following Hamilton's concepts, disputing the idea of evolutionary progress, and attacking the then widespread theory of group selection. Williams argued that natural selection worked by changing the frequency of alleles, and could not work at the level of groups.[90][86] Gene-centred evolution was popularised by Richard Dawkins in his 1976 book The Selfish Gene and developed in his more technical writings.[91][92]

Wilson's sociobiology, 1975

Ant societies have evolved elaborate caste structures, widely different in size and function.

Main article: Sociobiology

In 1975, E. O. Wilson published his controversial[93] book Sociobiology: The New Synthesis, the subtitle alluding to the modern synthesis[87] as he attempted to bring the study of animal society into the evolutionary fold. This appeared radically new, although Wilson was following Darwin, Fisher, Dawkins and others.[87] Critics such as Gerhard Lenski noted that he was following Huxley, Simpson and Dobzhansky's approach, which Lenski considered needlessly reductive as far as human society was concerned.[94] By 2000, the proposed discipline of sociobiology had morphed into the relatively well-accepted discipline of evolutionary psychology.[87]

Lewis's homeotic genes, 1978

Evolutionary developmental biology has formed a synthesis of evolutionary and developmental biology, discovering deep homology between the embryogenesis of such different animals as insects and vertebrates.

Main article: Evolutionary developmental biology

In 1977, recombinant DNA technology enabled biologists to start to explore the genetic control of development. The growth of evolutionary developmental biology from 1978, when Edward B. Lewis discovered homeotic genes, showed that many so-called toolkit genes act to regulate development, influencing the expression of other genes. It also revealed that some of the regulatory genes are extremely ancient, so that animals as different as insects and mammals share control mechanisms; for example, the Pax6 gene is involved in forming the eyes of mice and of fruit flies. Such deep homology provided strong evidence for evolution and indicated the paths that evolution had taken.[88]

Later syntheses

In 1982, a historical note on a series of evolutionary biology books[f] could state without qualification that evolution is the central organizing principle of biology. Smocovitis commented on this that "What the architects of the synthesis had worked to construct had by 1982 become a matter of fact", adding in a footnote that "the centrality of evolution had thus been rendered tacit knowledge, part of the received wisdom of the profession".[95]

By the late 20th century, however, the modern synthesis was showing its age, and fresh syntheses to remedy its defects and fill in its gaps were proposed from different directions. These have included such diverse fields as the study of society,[87] developmental biology,[50] epigenetics,[96] molecular biology, microbiology, genomics,[3] symbiogenesis, and horizontal gene transfer.[97] The physiologist Denis Noble argues that these additions render neo-Darwinism in the sense of the early 20th century's modern synthesis "at the least, incomplete as a theory of evolution",[97] and one that has been falsified by later biological research.[97]

Michael Rose and Todd Oakley note that evolutionary biology, formerly divided and "Balkanized", has been brought together by genomics. It has in their view discarded at least five common assumptions from the modern synthesis, namely that the genome is always a well-organised set of genes; that each gene has a single function; that species are well adapted biochemically to their ecological niches; that species are the durable units of evolution, and all levels from organism to organ, cell and molecule within the species are characteristic of it; and that the design of every organism and cell is efficient. They argue that the "new biology" integrates genomics, bioinformatics, and evolutionary genetics into a general-purpose toolkit for a "Postmodern Synthesis".[54]

Pigliucci's extended evolutionary synthesis, 2007

Main article: Extended evolutionary synthesis

In 2007, more than half a century after the modern synthesis, Massimo Pigliucci called for an extended evolutionary synthesis to incorporate aspects of biology that had not been included or had not existed in the mid-20th century.[98][99] It revisits the relative importance of different factors, challenges assumptions made in the modern synthesis, and adds new factors[99][100] such as multilevel selection, transgenerational epigenetic inheritance, niche construction, and evolvability.[101][96][102]

Koonin's 'post-modern' evolutionary synthesis, 2009

A 21st century tree of life showing horizontal gene transfers among prokaryotes and the saltational endosymbiosis events that created the eukaryotes, neither fitting into the 20th century's modern synthesis

In 2009, Darwin's 200th anniversary, the Origin of Species' 150th, and the 200th of Lamarck's "early evolutionary synthesis",[3] Philosophie Zoologique, the evolutionary biologist Eugene Koonin stated that while "the edifice of the [early 20th century] Modern Synthesis has crumbled, apparently, beyond repair",[3] a new 21st-century synthesis could be glimpsed. Three interlocking revolutions had, he argued, taken place in evolutionary biology: molecular, microbiological, and genomic. The molecular revolution included the neutral theory, that most mutations are neutral and that negative selection happens more often than the positive form, and that all current life evolved from a single common ancestor. In microbiology, the synthesis has expanded to cover the prokaryotes, using ribosomal RNA to form a tree of life. Finally, genomics brought together the molecular and microbiological syntheses - in particular, horizontal gene transfer between bacteria shows that prokaryotes can freely share genes. Many of these points had already been made by other researchers such as Ulrich Kutschera and Karl J. Niklas.[103]

Towards a replacement synthesis

Inputs to the modern synthesis, with other topics (inverted colours) such as developmental biology that were not joined with evolutionary biology until the turn of the 21st century[103]

Biologists, alongside scholars of the history and philosophy of biology, have continued to debate the need for, and possible nature of, a replacement synthesis. For example, in 2017 Philippe Huneman and Denis M. Walsh stated in their book Challenging the Modern Synthesis that numerous theorists had pointed out that the disciplines of embryological developmental theory, morphology, and ecology had been omitted. They noted that all such arguments amounted to a continuing desire to replace the modern synthesis with one that united "all biological fields of research related to evolution, adaptation, and diversity in a single theoretical framework."[104] They observed further that there are two groups of challenges to the way the modern synthesis viewed inheritance. The first is that other modes such as epigenetic inheritance, phenotypic plasticity, the Baldwin effect, and the maternal effect allow new characteristics to arise and be passed on and for the genes to catch up with the new adaptations later. The second is that all such mechanisms are part, not of an inheritance system, but a developmental system: the fundamental unit is not a discrete selfishly competing gene, but a collaborating system that works at all levels from genes and cells to organisms and cultures to guide evolution.[105]

Historiography

Looking back at the conflicting accounts of the modern synthesis, the historian Betty Smocovitis notes in her 1996 book Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology that both historians and philosophers of biology have attempted to grasp its scientific meaning, but have found it "a moving target";[106] the only thing they agreed on was that it was a historical event.[106] In her words

"by the late 1980s the notoriety of the evolutionary synthesis was recognized ... So notorious did 'the synthesis' become, that few serious historically minded analysts would touch the subject, let alone know where to begin to sort through the interpretive mess left behind by the numerous critics and commentators".[107]

See also

Developmental systems theory
Gene-centered view of evolution
History of evolutionary thought
Neo-Darwinism
Objections to evolution

Notes

^ Also known variously as the New person, the Modern Evolutionary Synthesis, the Evolutionary Synthesis, and the neo-Darwinian Synthesis. These alternative terms are ambiguous as they could possibly include later syntheses, so this article uses Julian Huxley's 1942 "modern synthesis"[2] throughout.
^ Peter Gauthier has however argued that Weismann's experiment showed only that injury did not affect the germplasm. It did not test the effect of Lamarckian use and disuse.[14]
^ Morgan's work with fruit flies helped establish the link between Mendelian genetics and the chromosomal theory of inheritance, that the hereditary material was embodied in these bodies within the cell nucleus.[34]
^ Fisher also analysed sexual selection in his book, but his work was largely ignored, and Darwin's case for such selection misunderstood, so it formed no substantial part of the modern synthesis.[42]
^ Though C. H. Waddington had called for embryology to be added to the synthesis in his 1953 paper "Epigenetics and Evolution".[52]
^ In a reissue of Dobzhansky's Genetics and the Origin of Species.

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Biologia evolutiva

Cronologia

de l'evolució
Història de l'índex de vida

Evolució

Abiogènesi
Adaptació
Radiació adaptativa
Cladística
Coevolució
Descens comú
Divergència

Més aviat coneguda Formes
de vida Evidència de l'evolució

Extinció Esdeveniment

Centrat en gens
Veure Homologia
Últim avantpassat comú universal
Macroevolució Microevolució

Radiació no adaptativa
Origen de la vida
Panspèrmia
Evolució paral·lela
Taxonomia d'especiació

Genètica de poblacions

Biodiversitat Flux
genètic
Deriva genètica
Mutació
selecció natural Selecció
artificial
Variació
Selecció sexual
Selecció social

Desenvolupament

Canalització
Biologia evolutiva del desenvolupament
Assimilació genètica
Inversió
Modularitat
Plasticitat fenotípica

De tàxons

Bacteris
Aus

origen

Braquiòpodes
Mol·luscs

Cefalòpodes

Dinosaures
Peixos
Fongs
Insectes

Papallones

Vida
Mamífers

gats
cànids

llops
gossos

hienes
dofins i balenes
cavalls
Cangur

primats
humans
lèmurs

marins

Plantes
Rèptils
Aranyes
Tetràpodes
Virus

de la grip

Dels òrgans

ADN
cel·lular
Flagella
Eucariotes

simbiosi
cromosoma
endomembrana sistema
mitocondri
nucli
plastidis

En animals

pèl
ocular
ossicle auditiu
nerviós cervell del sistema

De processos

Envelliment

Mort cel
·lular programada vol

aviari Vol
biològic
Cooperació
Visió
del color

en primats

Emoció Empatia
Ètica
Eusocialitat
Sistema immunitari
Metabolisme
Monogàmia
Moralitat
Mosaic evolució
Multicel·lularitat
Reproducció sexual

Diferenciació/sexes

Cicles de vida/fases nuclears
Aparellament tipus
Meiosi
Determinació del sexe

Verí de serp

Tempo i modes

Gradualisme/Equilibri puntuat/Saltacionisme
Micromutació/Uniformitarisme de Macromutacions
/Catastrofisme

Especiació

Anagènesi
al·lopàtrica
Catagènesi
Cladogènesi
Cospeciation
Híbrid Ecològic

Parapàtric
Peripàtric
Reforç
Simpàtric

Història

Renaixement i Il·lustració
Transmutació de l'espècie
David Hume

Diàlegs sobre la religió natural

Charles Darwin

Sobre l'origen de les espècies

Història de la paleontologia
Fòssil de transició
Barreja de l'herència
mendeliana
L'eclipsi del darwinisme
Síntesi moderna
Història de l'evolució molecular
Síntesi evolutiva estesa

Filosofia

Darwinisme

Alternatives Catastròfic
Lamarckisme
Ortogènesi
Mutacionisme
Saltacionisme
Estructuralisme

Spandrel

Teista
Vitalisme

Teleologia en biologia

Relacionat

Biogeografia
Genètica ecològica
Evolució molecular
Astrobiologia
Filogenètica

Polimorfisme d'arbres

Protocell

Systematics

Categoria
Commons
Portal
Viquiprojecte

Control d'autoritats: Biblioteques nacionals

Alemanya