Chance, Selection, and the Mendelians

Mendel @ 200, 21/7/2022

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The Rise of Chance in Evolutionary Theory

A Pompous Parade of Arithmetic

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.





A shift to a statistical theory of evolution, which could let us understand the action of natural selection across generations, at the population level, which could be harmonized with Mendelian transmission

The Classic Story



According to the classic story:

At least for natural selection and evolution, the arrival of Mendel is **a bad thing**. We spend fifty years worried about **gradualism versus saltationism** and fail to integrate **statistics and chance** into a Mendelian perspective





While G. Udny Yule followed "the approach of population genetics," nonetheless "conflicts among his contemporaries prevented its development at this time." (Provine)

The "personal quarrel" between Bateson and Weldon "certainly delayed the utilization of the powerful methods of statistics in much of genetics." (Sturtevant) The take-home message: The period from 1880–1930 is *much* more exciting than that! There's a blooming, buzzing confusion of excitement around evolutionary methods, with much work toward a common, synthetic goal.

The Non-Mendelian Tradition



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The Non-Mendelian Traditio

W. F. R. Weldon (1860-1906)

Good old Galton's stirp, in which some of the ancestral characters are latent, is still the only "machine" which will work: and the proper line of research is an enquiry into those embryonic stimuli which make a given character evident or latent. That is my fixed belief. (Weldon, 1904)

The Mendelians



William Bateson (1861–1926)

Of the so-called investigations of heredity pursued by extensions of Galton's non-analytical method and promoted by Professor Pearson and the English Biometrical school it is now scarcely necessary to speak. [...] To those who hereafter may study this episode in the history of biological science it will appear inexplicable that work so unsound in construction should have been respectfully received by the scientific world. (Bateson 1909)

William Bateson (1861–1926)

Galton said to me that Pearson can understand Bateson, but Bateson *cannot* understand Pearson. (Leonard Darwin to Fisher, April 27, 1928)

But things are different elsewhere!

Piecemeal Advances

- Statistical methods without a statistical theory of inheritance (merely for data analysis): William Castle (MacCurdy and Castle, 1907); Wilhelm Johannsen (1909)
- Mathematical inheritance without statistical methods (recurrence equations): Herbert Spencer Jennings (1912–6), Robbins (1917–8), Howard C. Warren (1917)
- Estimations of the speed of selection: Harry Norton and R.C. Punnett (1915)
- Statistical inheritance without natural selection: Herman Nilsson-Ehle (1908), Edward Murray East (1910–3)

(17) The population at the beginning consists of AA and Aa in equal numbers. After *n* assortative matings (including among these the first mating, where all are dominants), the proportions are as follows:

$$AA = \frac{3n+6}{4n+12}; \text{ thus } \frac{9}{16}, \frac{12}{20}, \frac{15}{24}, \frac{18}{28}, \dots, \frac{3}{4}, AA_{72} = .740.$$

$$aa = \frac{n}{4n+12}; \text{ thus } \frac{1}{16}, \frac{2}{20}, \frac{3}{24}, \frac{4}{28}, \dots, \frac{1}{4}. \quad aa_{72} = .240.$$

$$Aa = \frac{6}{4n+12}; \text{ thus } \frac{6}{16}, \frac{6}{20}, \frac{6}{24}, \frac{6}{28}, \dots, 0. \quad Aa_{147} = .010.$$

$$Dominants = \frac{3n+12}{4n+12}; \quad \text{recessives} = \frac{n}{4n+12}.$$

Jennings (1916)

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Percentage of total population formed by old variety	Percentage of total population formed by the hybrids	Percentage of total population formed by the new variety	Number of generations taken to pass from one position to another as indicated in the percentages of different individuals in left-hand column							
			A. Where the new variety is dominant				B. Where the new variety is recessive			
			1 <u>00</u> 50	1 <u>00</u> 75	<u>100</u> 90	100	100 50	$\frac{100}{75}$	100 100	100 99
$\begin{array}{c} 99 \cdot 9 \\ 98 \cdot 0 \\ 90 \cdot 7 \\ 69 \cdot 0 \\ 44 \cdot 4 \\ 25 \cdot \\ 11 \cdot 1 \\ 2 \cdot 8 \\ \cdot 03 \\ \cdot 008 \\ \cdot 000 \end{array}$	$\begin{array}{c} \cdot 09\\ 1\cdot 96\\ 9\cdot 0\\ 27\cdot 7\\ 44\cdot 4\\ 50\cdot \\ 44\cdot 4\\ 27\cdot 7\\ 9\cdot 0\\ 1\cdot 96\\ \cdot 09\end{array}$	$\begin{array}{c} \cdot 000\\ \cdot 008\\ \cdot 03\\ 2 \cdot 8\\ 11 \cdot 1\\ 25 \cdot \\ 44 \cdot 4\\ 69 \cdot 0\\ 90 \cdot 7\\ 98 \cdot 0\\ 99 \cdot 9\end{array}$	$egin{array}{c} 4\\ 2\\ 2\\ 2\\ 2\\ 4\\ 10\\ 36\\ 170\\ 3840 \end{array}$	$10 \\ 5 \\ 4 \\ 4 \\ 4 \\ 8 \\ 17 \\ 68 \\ 333 \\ 7653$	$28\\15\\14\\12\\12\\18\\40\\166\\827\\19,111$	$\begin{array}{r} 300\\ 165\\ 153\\ 121\\ 119\\ 171\\ 393\\ 1,632\\ 8,243\\ 191,002 \end{array}$	1920 85 18 5 2 2 2 2 2 4	5740 250 51 13 6 4 4 6 6 10	$17,200 \\ 744 \\ 149 \\ 36 \\ 16 \\ 11 \\ 11 \\ 14 \\ 16 \\ 28$	$189,092 \\ 8,160 \\ 1,615 \\ 389 \\ 169 \\ 118 \\ 120 \\ 152 \\ 165 \\ 299$

Punnett (1915)

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A MENDELIAN INTERPRETATION OF VARIA-TION THAT IS APPARENTLY CONTINUOUS¹

PROFESSOR EDWARD M. EAST

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THERE are two objects in writing this paper. One is to present some new facts of inheritance obtained from pedigree cultures of maize; the other is to discuss the hypotheses to which an extension of this class of facts naturally leads. This discussion is to be regarded simply

The Textbook Tradition

RECENT PROGRESS IN THE STUDY OF VARIATION, HEREDITY, AND EVOLUTION

By ROBERT HEATH LOCK, M.A.

FELLOW OF GONVILLE AND CAIUS COLLEGE, CAMBRIDGE

HEREDITY

By J. ARTHUR THOMSON, M.A.

Regius Professor of Natural History in the University of Aberdeen

AUTHOR OF "THE STUDY OF ANIMAL LIFE," "THE SCIENCE OF LIFE," "OUTLINES OF ZOOLOGY," "THE PROGRESS OF SCIENCE," "HERBERT SPENCER," ETC.; JOINT-AUTHOR OF "THE EVOLUTION OF SEX"

HEREDITY



What's There?

- Careful, reasonable presentations of both biometry and Mendelism
- No indication of a hefty conflict between them
- A **genuine desire** to unify biology, along broadly the lines we've already seen



Questions?

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Extra Slides

Weldon: Early Selection

For by purely statistical methods, without making any assumption as to the functional importance of the frontal breath, the time of life at which natural selection must be assumed to act, if it acts at all, has been determined, and the selective death-rate has been exhibited as a function of the abnormality... (Weldon, 1895a, p. 371)

Weldon: Shift

The whole difficulty of the theory of Natural Selection is a quantitative difficulty. It is a difficulty of believing that in any given case a small deviation from the mean character will be sufficiently useful or sufficiently harmful to matter. [...] For numerical knowledge of this kind is the only ultimate test of the theory of Natural Selection, or of any other theory of any natural process whatever. (Weldon, 1898, p. 902)

Yule on Mendelism

The value of the work of Mendel and his successors lies not in discovering a phenomenon inconsistent with that law [of ancestral heredity], but in shewing that a process, consistent with it, though neither suggested nor postulated by it, might actually occur. (Yule, 1902, p. 227)

Yule on Biometry

What is required from a physical theory of heredity is that it should assign a meaning to the variations in the constants that do occur, enabling one, given the law of ancestral heredity for an organ, to state the relative influences thereon of the different agencies concerned—selection, in all forms, circumstance, and so forth. (Yule, 1902, p. 237)