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The Implications and Purposes of Early Experimental Evolution[1]

The history of evolutionary studies is told primarily as a history of ideas, emphasizing the roles of observation and theory.[2] But biology is not only about names, classification, and geography; it is also about control, manipulation, and intervention. As historians have demonstrated, at the turn of the twentieth century, biologists across many subdisciplines experimentalized their science. Embryologists, for example, first created time-slices of developing organisms for the purpose of standardizing the process of growth, as well as traced the lineages of cells, but before long, figures like Wilhelm Roux began to directly manipulate embryos under artificial conditions.[3] Physiologists had developed their science in parallel and from it emerged a figure like Jacques Loeb, whom Pauly labeled the "biologist-engineer," whose explicit goal was to take control of life.[4] For these scientists, to intervene was to understand.[5] Indeed, following Philip Pauly's biography of Loeb, historians such as Lily Kay, Sharon

[1] This paper is a draft. To cite, permission by the author is required. The submitted abstract indicated more of a focus on eugenics, but I found it too difficult to incorporate into this paper, in terms of both logic and time. See footnotes 19 and 49 for more discussion of eugenics.

[2] Because "history of evolution" can mean the history of evolution of life over billions of years or the history of evolution as a field of inquiry, I refer to the latter as "evolutionary studies." I chose to avoid "evolutionary biology" because that is usually the name of the discipline; "evolutionary studies" is an analytical category.

[3] Maienschein, Jane, *Whose View of Life? Embryos, Cloning, and Stem Cells* (Cambridge: Harvard University Press, 2005).

[4] Pauly, Philip, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987). For a summary, see my blog post at: https://phylogenous.wordpress.com/2015/04/14/book-thoughts-paulys-controlling-life/

[5] This kind of argument is developed by Ian Hacking and Lily Kay. Hacking, Ian, *Representing and Intervening* (Cambridge: Cambridge University Press, 1983); Kay, Lily E., *The Molecular Vision of Life: Caltech, the Rockefeller Foundation, and the Rise of the New Biology* (New York: Oxford University Press, 1993).

Kingsland, and Adele Clarke, tied the experimentalization of biology, including genetics, ecology, and molecular biology, to a desire for control.[6] In this talk, I will focus on the experimentalization and control of a biological process that has not received its fair study: evolution.

As much as historians have focused on experimentalization, control, and evolution, the interplay of these threads has yet to be fully explored. The most extensive studies of experimental evolution remain Robert Kohler's *Landscapes and Labscapes* (2002) and Sharon Kingsland's "The Battling Botanist" (1991), which are 13 and 24 years old, respectively.[7] In general, philosophers have appeared to be more interested in experimental evolution, including Jean Gayon and David Rudge, who have studied developments later in the century.[8] (Recent works by Luis Campos and Helen Curry possibly indicate a returning interest to the topic,

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6 Kay, *The Molecular Vision of Life*; Clarke, Adele E., *Disciplining Reproduction: Modernity, American Life Sciences, and "the Problems of Sex"* (Berkeley: University of California Press, 1998); Kingsland, Sharon E., *The Evolution of American Ecology, 1890-2000* (Baltimore: The Johns Hopkins University Press, 2005).

7 Kohler, Robert E., *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology* (Chicago: University of Chicago Press, 2002); Kingsland, Sharon E., "The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900-1912," *Isis*, 1991, 82, no. 3:479-509. Unlike Kingsland, Kohler is not so much concerned with "control," but with the ambiguous "place" practitioners of experimental evolution and experimental ecology found themselves: the "border" between the laboratory and the field. In this sense, playing off Kohler, perhaps my interpretation of experimental evolution makes it a "border science" in that it is not tied to a "place" (here, a discipline).

8 Jean Gayon has written about the work of L'Héretier and Teissier, French biologists who were the first to test theories of population genetics. Gayon, Jean, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Selection* (Cambridge University Press, 2007); Gayon, Jean and Michel Veuille, "The Genetics of Experimental Populations: L'héritier and Teissier's Population Cages," in *Thinking About Evolution: Historical, Philosophical, and Political Perspectives*, eds. Rama S. Singh, et al. (Cambridge University Press, 2001); Gayon, Jean, "Darwin and Darwinism in France after 1900," in *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, ed. Michael Ruse (Cambridge University Press, 2013). Philosophers of science have also examined some work in experimental evolution: Rudge, David Wÿss, "The Complementary Roles of Observation and Experiment: Theodosius Dobzhansky's Genetics of Natural Populations Ix and Xii," *History and Philosophy of the Life Sciences*, 2000, 22:167-86; Wilner, Eduardo, "Darwin's Artificial Selection as an Experiment," *Studies in History and Philosophy of Biological and Biomedical Sciences*, 2006, 37:26-40; Pigliucci, Massimo, "The Nature of Evolutionary Biology: At the Borderlands between Historical and Experimental Science," in *The Philosophy of Biology: A Companion for Educators*, ed. Kostas Kampourakis (Springer, 2013).

however.)[9] Because of this paucity, the degree to which experimentation has generally influenced the historical development of evolutionary studies, as well as how biologists have sought to control the process itself, remain unclear.[10] As I begin this project to explore the history of experimental evolution, I want to present to you some of its early history, with two important conclusions: First, the history of experimental evolution is not the history of the discipline of evolutionary biology; instead, it appears that it is something[11] biologists employ to better understand their own disciplines, such as ecology and genetics, both of which I discuss today. Second, as these biologists developed their sciences, the methods by which they could control evolution fluctuated with consequence. Ever present, however, was the desire to control evolution — a desire first expressed scientifically, I think, in 1891.

In 1891, the French Darwinian Henry de Varigny called for an "experimental evolution."[12] Worried that much of the public still denied its reality, he hoped that scientists could create a new species "through direct experiment, through experimental transformism." In addition, de Varigny, writing during the so-called "eclipse of Darwinism," argued that experimentalization would help biologists advance a science bogged down by competing speculative theories. Doing so would assist not only scientists, for he also cited breeders as a kind of 'experimental evolutionist,' pointing to the practical and economic benefits that would result from its pursuit.

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[9] Curry, Helen Anne, "Accelerating Evolution, Engineering Life: American Agriculture and Technologies of Genetic Modification, 1925-1960" (Ph.D. Dissertation, Yale, 2012); Campos, *Radium and the Secret of Life*.

[10] This question is not so much a mystery for biological disciplines that are intervention-based in which many of the most well-known figures were experimentalists. In contrast, evolution - a "border science" in Kohler's terms - had a troubled relationship with experimentation (and continues to do so) that is difficult to parse. An important point is that the history of experimental evolution is not a history of the discipline of evolutionary biology; instead, those engaged in the practice were primarily affiliated with other disciplines.

[11] I have not yet figured out how to characterize it. Is it a method, a perspective, a drive?

To jump-start experimental evolution, de Varigny called for the construction of a research institute equipped with farms and laboratories designed for the purpose of long-term experimentation, allowing for the study of evolutionary processes in real-time.[13] Twelve years later, at Cold Spring Harbor, New York, the Carnegie Institution of Washington established the Station for Experimental Evolution. At its 1904 inauguration, the premier experimental evolutionist of the time, Hugo de Vries, addressed the station's patrons, saying,

> "We want to have a share in the work of evolution, since we partake of the fruit. We want even to shape the work, in order to get still better fruits. … First, it [evolution] must be controlled and studied, afterwards conducted along selected lines, and finally shaped to the use of man."

Its director, Charles Davenport, wrote of the station's purpose:

> "Since when we know the law we may control the process, the principles of evolution will show the way to an improvement of the human race." "It ["such knowledge"] shows how organisms may be best modified to meet our requirements of beauty, food, materials, and power."

Thus De Varigny, de Vries, and Davenport expounded the goals of experimental evolution. They cited Francis Bacon's utopian novel *New Atlantis*, indicating that experimental evolution was to have the dual purpose of understanding the mechanisms by which life evolves as well as the mastery thereof.[14] By studying and manipulating evolution's causes as they occurred, rather than **its** history, scientists might get a handle on the process itself. I interpret the history of experimental evolution, therefore, as how scientists sought to not only understand evolution, but to *control* it.

In 1905, an independent voice also called for the experimentalization of evolution: the

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[12] De Varigny, Henry, *Experimental Evolution* (MacMillan and Co., 1892).

[13] G. J. Romanes and Charles Davenport also expressed this, as discussed by Kohler. Kohler, *Landscapes and Labscapes*, pp. 44-46.

[14] For more on the relationship between Francis Bacon and experimental evolution, see my blog post at

grassland ecologist, Frederic Clements. While he is known most famously for his theory of ecological succession and his drive to experimentalize ecology, he attempted the same with regard to evolution. He, too, cited Bacon, and his methods parallel Bacon's own suggestions. A neo-Lamarckian, Clements thought the habitat was "the motive force in control" of evolution[15], and dismissed the mechanisms of competing theories as either too rare or too slow.[16] Clements' mechanistic physiology determined that "natural selection does not operate upon the forms produced by adaptation, since they are immediately in harmony with the environment that produces them."[17] To demonstrate this, Clements transplanted grasses and flowers from one kind of habitat to another, usually at different altitudes. By doing so, he found that species immediately adapted to their environment, sometimes even changing to resemble a closely related species.[18] Finding that such conversions occurred in a wide range of plants, Clements' experiments confirmed his neo-Lamarckian theory of evolution.[19]

Unlike other kinds of experiment, Clements worked within an ecological context in which it was difficult to control for all variables, and his efforts to do so seem to have failed, for

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https://phylogenous.wordpress.com/2014/05/01/francis-bacon-the-father-of-experimental-evolution/

15 {Clements, 1924}

16 Clements, Frederic E., *Plant Physiology and Ecology* (Henry Holt and Company, 1907). Regarding competing theories of evolution, he rejected mutations as unimportant due to their rarity and he rejected Darwin's theory of variation because he thought it too slow and unproven.

17 Clements, Frederic E., Emmett V. Martin, and Frances L. Long, *Adaptation and Origin in the Plant World: The Role of Environment in Evolution* (The Chronica Botanica Company, 1950). I am citing across the wide span of time, but Clements, as far as I can tell, remained remarkably consistent in his evolutionary views across the decades.

18 For example, by transplanting nodding ragwort from its naturally sunny habitat to a shaded one, he thought it converged into another species, the bashful ragwort.

19 While Sharon Kingsland has clarified the social purposes of Clements' experimental ecology - the sustainable land development of the American Midwest - it is not clear for what reason he pursued experimental evolution besides an understanding of the process. Kingsland, *The Evolution of American Ecology, 1890-2000*. Citing a letter, Ronald Tobey argues Clements' rejection of genetics was partially due to the eugenics promoted in its name. Clements' writings are permeated with "control" talk, but in the context of how environmental mechanisms such as humidity and light influence plant growth, mechanisms which do not readily analogize to humans and human society. He instead emphasized the improvement of human environments to improve the race, a view shared by many neo-Larmarckians. Tobey, Ronald C., *Saving the Prairies: The Life Cycle of the Founding School of American*

eventually, his methodological descendants - the experimental taxonomists - discredited his theoretical conclusion on the grounds of environmental contamination.[20] As Robert Kohler witnessed in the tragic career of William Tower, conducting experimental evolution in the field - at this time, anyway - was a somewhat hopeless endeavor[21], even if it meant less work to bridge the natural/artificial divide, a common critique of experimental evolution.[22] To control evolution, a scientist needs to also control as many variables as possible. (I will note in passing that this hints at two important meanings of control: Control as a constraint upon variables - essential to experimental design; and control as the manipulating to produce a novel result.) The geneticists, by working in agricultural fields and laboratories, would not allow for complexity to endanger their experimental designs and results.

The scientific work surrounding experimental breeding, Mendelian genetics, and the pure line theory was truly Baconian: as many historians have written, including Barbara Kimmelman, Diane Paul, and Deborah Fitzgerald, these sciences developed for a blend of reasons both "pure" and "applied."[23] The first response to de Varigny's challenge, in fact, was from a horticulturist: In 1895, Liberty Hyde Bailey argued, in "Experimental Evolution Amongst Plants," that domestication was

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Plant Ecology, 1895-1955 (University of California Press, 1981).

[20] Hagen, Joel, "Experimentalists and Naturalists in Twentieth-Century Botany: Experimental Taxonomy, 1920-1950," *Journal of the History of Biology*, 1984, 17, no. 2:249-70.

[21] Kohler, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology*.

[22] This is a huge theme that I mention only here. For an excellent discussion of the distinction between artificial and natural, see Andrew Inkpen's dissertation. Inkpen, S. Andrew, "Denaturing Nature: Philosophical and Historical Reflections on the Artificial-Natural Distinction in the Life Sciences" (Ph.D. Dissertation, The University of British Columbia, 2014).

[23] Fitzgerald, Deborah, *The Business of Breeding: Hybrid Corn in Illinois, 1890-1940* (Cornell University Press, 1990); Paul, Diane B. and Barbara Kimmelman, "Mendel in America: Theory and Practice, 1900-1917," in *The Expansion of American Biology*, ed. Keith R. Benson, Jane Maienschein, and Ronald Rainger (Rutgers University Press, 1988).

"the experiment to prove that evolution is true, worked out upon a scale and with a definiteness of detail which the boldest experimenter could not hope to attain, were he to live a thousand years. The horticulturist is the only man in the world whose distinct business and profession is evolution. He, of all other men, has the experimental proof that species come and go."[24]

But experimental breeding not only demonstrated evolution, its interventionism provided insights into how to understand and control it. Indeed, Charles Darwin, who used the work of breeders to develop his theory of natural selection as well as to discover the laws of variation and heredity, called domestication "an experiment on a gigantic scale."[25] A problem with Darwin's theory of evolution, however, is that it left the generation of variation somewhat mysterious. The properties he ascribed to variations - particularly their minuteness - rendered them difficult to analyze. (And of course, the swamping effect to which Darwinism was prone would also hinder the control of evolution.) Unless one had the statistical rigor of Raphael Weldon, evolution could be intractable if an entire mechanism was beyond experimental study.[26] The first geneticists instead emphasized discontinuities in variation partially for these reasons. The leading geneticist William Bateson wrote in 1909 that:

"By suggesting that the steps through which an adaptive mechanism arose were indefinite and insensible, all further trouble is spared. While it could be said that species arise by an insensible and imperceptible process of variation, there was clearly no use in tiring ourselves by trying to perceive that process."[27]

Indeed, an advantage of the mutations upon which geneticists focused was that they were

[24] Bailey, Liberty Hyde, "Experimental Evolution Amongst Plants," *The American Naturalist*, 1895, 29, no. 340:318-25. For more on Bailey's article, see my blog post at https://phylogenous.wordpress.com/2014/06/30/experimental-evolution-amongst-plants-1895/

[25] For a discussion of Darwin's use of experimental breeding, see Wilner, "Darwin's Artificial Selection as an Experiment."

[26] For more on Weldon, see Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Selection*; Ruse, Michael, *Monad to Man* (Harvard University Press, 1996).

[27] Bateson, William, "Heredity and Variation in Modern Light," in *Darwin and Modern Science*, ed. A. C. Seward (Cambridge University Press, 1909).

distinguishable and observable, but this did not mean they were necessarily controllable. While Hugo de Vries had advocated for such control, the mutation theory itself did not elaborate upon how to do so: in fact, de Vries had himself struggled to find species in the active process of mutation, basing his experimental work on only the evening primrose.[28] His concept of a "mutation period" left the process outside human control. Daniel MacDougal, the "Battling Botanist" about whom Sharon Kingsland and Luis Campos have written extensively, worried that the primrose's mutation period could soon end, leaving biologists without an organism upon which to validate and elaborate the mutation theory.[29] Given that de Vries pointed to mutation as evolution's creative agency, MacDougal sought to artificially induce mutations by a variety of means, including chemicals and radiation.[30] Later, in 1912, Edwin Conklin worried that a failure to do so would hinder the control of evolution, writing,

> "If changes in the germplasm may be induced by extrinsic conditions, then a real experimental evolution will be possible; if they can not be so induced we can only look on while the evolutionary processes proceed, selecting here and there a product which nature gives us, but unable to initiate or control these processes."[31]

MacDougal did indeed create mutations, but biologists did not reliably induce them to a practical degree until the mid-1920s. For more on experimental studies of mutation, I refer you to the works of Luis Campos and Helen Anne Curry.[32]

The significance that biologists attached to the induction of mutations can perhaps be

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[28] I have noticed that historians frequently accuse De Vries of having only built his mutation theory upon only *Oenothera lamarckiana*, but I do not think this is quite accurate. De Vries, in *Die Mutationstheorie,* has many observations of plants in the wild whose diversity he thinks can be explained by his framework.

[29] Campos, Luis, *Radium and the Secret of Life* (University of Chicago Press, 2015), p. 108.

[30] For more on creativity, see Cable, Kele, "The History of the Creative Force of Evolution," (unpublished manuscript, 2011).

[31] Conklin, Edwin G., "Problems of Evolution and Present Methods of Attacking Them," *The American Naturalist*, 1912, 46, no. 543: p. 126.

[32] Curry, Helen Anne, "Accelerating Evolution, Engineering Life: American Agriculture and Technologies of Genetic Modification, 1925-1960" (Ph.D. Dissertation, Yale, 2012); Campos, *Radium and the Secret of Life*.

interpreted as a response to the faltering status of natural selection as the source of evolution's creativity.[33] An irony in the history of experimental evolution is that many of the first selection experiments, the primary method in today's science, instead demonstrated that selection had a limited power in causing evolutionary change. The experiments that did so were first conducted by the Danish biologist Wilhelm Johannsen, who Gayon and Zallen argue, developed the pure line theory in response to problems encountered by plant breeders, especially that of Louis de Vilmorin.[34] In the mid-19th century, de Vilmorin had failed to improve his crops via the traditional method of mass selection. To break this stall, he developed the pedigree method, in which instead of evaluating an individual by its ancestry, as was traditionally done, he evaluated it by its progeny.[35] In 1903, Johannsen, inspired by de Vilmorin, Hugo de Vries, and Francis Galton, synthesized biometric methods with the pedigree method so that he could perform a crucial experiment between Darwinism and mutationism.[36] From his experiments he produced a theory which stated that natural selection can only/merely isolate pre-existing pure lines; any evolutionary change had to instead occur through internal mutations, large or small.[37] The genotype-phenotype distinction he later articulated further contradicted the evolutionary theories of both Darwinians and neo-Lamarckians. By controlling both the environment and the breeding of his organisms, Johannsen was capable of making distinctions not available to a scientist like

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[33] Cable, "The History of the Creative Force of Evolution."

[34] Gayon, Jean and Doris T. Zallen, "The Role of the Vilmorin Company in the Promotion and Diffusion of the Experimental Science of Heredity in France, 1840-1920," *Journal of the History of Biology*, 1998, 31, no. 2:241-62.

[35] This is a break from traditional methods because, contrary to Galton's and Pearson's law of ancestral heredity, an individual's ancestry was not what determined their traits, but what their own genetic make-up was, which was easier to determine through examining its progeny instead.

[36] This is simplistic, but it will do for my purposes. Roll-Hansen, Nils, "The Crucial Experiment of Wilhelm Johannsen," *Biology and Philosophy*, 1989, 4:303-29.

[37] Johannsen's experiment is described in many works. See Stoltzfus, Arlin and Kele Cable, "Mendelism-Mutationism: The Forgotten Evolutionary Synthesis," *Journal of the History of Biology*, 2014, 47, no. 4:501-46.

Frederic Clements who had worked with the complex ecology of the field.[38]

Herbert Spencer Jennings, who in 1908 confirmed Johannsen's results in *Paramecia*, worried over the implications of the pure line theory.

> "We must consider, …, that if the non-inheritable differences are so much more numerous and marked than the inheritable ones as to render conscious selection by human beings ineffective, they would apparently have the same effect on selection by the agencies of nature."[39]

That is, if most visible variation is generated by the environment, how could nature or humans select? What power could natural selection have?

Raymond Pearl put the pure line theory and the genotype-phenotype distinction to practical use, showing that not all hope was lost, but it *was* a challenge. Working at Maine's Agricultural Experiment Station on the problem of increasing the yields of egg-laying hens, Pearl discovered that the traditional mass selection method had actually slightly decreased yields over time. Following Johannsen, Pearl instituted the pedigree method, discovering that a group of hens who had produced high yields was actually composed of two approximate "pure lines" that when bred separately, showed a significant difference in average yield. Realizing that the environment generated variation which allowed the low pure line to sometimes produce high yields, but not pass it on to its offspring, Pearl isolated the low line from the high pure line, immediately improving yields: a practical result of experimental evolution. Indeed, Kathy Cooke argued that Pearl saw little distinction between "pure" and "applied" research: for example, Pearl measured fecundity during the winter months - the time in which eggs were priced at their

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[38] As Jan Sapp and Sharon Kingsland have pointed out, the work of the geneticists had two impacts regarding "control": First, their distinction between definite mutations and environmental fluctuations could cut through the mess of variations and allow for more evolutionary control; secondly, because of this distinction, geneticists were now in control of determining which traits were evolutionarily important and which were not.

[39] Jennings, Herbert S., "Heredity, Variation and Evolution in Protozoa II," *Proceedings of the American Philosophical Society*, 1908, 47, no. 190: pp. 511, 522. It is of interest to note that Jennings is directly extrapolating

highest - with the hope that farmers could increase their profits.[40]

In the mean time, the geneticist William Castle challenged the pure line theory, arguing that selection was far more effective than Johannsen, Jennings, and Pearl had claimed.[41] Working with piebald rats, Castle selected for more or less coverage of coat color beyond the range of what existed normally. Contrary to Johannsen's theory, which stated that genes were stable and immune to the environment and natural selection, Castle found that variation could be pushed beyond its normal limits. He concluded that selection itself caused the genes to vary. In doing so, Castle told the Carnegie Institution that he could "demonstrate the efficacy of mass selection" and was

> "led to conclude that selection is, in animal breeding, a more important agent than mutation, partly because it is *controllable* and its results therefore more certain, and partly because it may even *determine* the occurrence of mutations of a particular sort."[42]

The power Castle wished to lend to natural selection went beyond what Darwin thought, hoping that he could even influence the *direction* of mutation.

Even as evidence for the pure line theory continued to pour in, Castle maintained his stance throughout the 1910s.[43] Simultaneously, those who resisted Castle's interpretations began

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from artificial experiment to the workings of evolution in the wild.

[40] Cooke, Kathy J., "From Science to Practice, or Practice to Science? Chickens and Eggs in Raymond Pearl's Agricultural Breeding Research, 1907-1916," *Isis*, 1997, 88, no. 1:62-86. Additionally, Pearl realized that fecundity, while inherited, was subject to wide variation due to environmental effects, and so he advised farmers to continue practicing what they already knew: improving a hen's environment improves its egg-laying capacity. This hints at the limited impact genetics had upon agriculture that historians have discussed, but I did not have time to spend on here. For the latest word on the relationship between biology and agriculture, see Phillips, Denise and Sharon E. Kingsland, eds., *New Perspectives on the History of Life Sciences and Agriculture*, vol. 40, *Archimedes* (Springer, 2015).

[41] Provine, William B., *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971); Vicedo, Marga, "Realism and Simplicity in the Castle-East Debate on the Stability of the Hereditary Units: Rhetorical Devices Versus Substantive Methodology," *Studies in History and Philosophy of Science*, 1991, 22, no. 2:201-21.

[42] Carnegie Institution of Washington, Yearbook Vol. 12, 1913, pp. 116-117. Emphasis mine. Note that this is not a direct quote from Castle; the author of the passage (Davenport?) says this is what Castle has reported.

[43] Like Jennings, other biologists iterated Johannsen's pure line experiments throughout the kingdoms of life,

to realize how their own researches could give back to selection its power.[44] Castle's results were real, but his interpretation was faulty. Castle's opponents, including Edward East and the Drosophilists, applied reinterpreted Castle's results in the light of advances in Mendelian genetics, claiming that the extreme variations Castle produced were actually due to modifying factors. Castle was in fact not causing a gene to vary, but eliminating the factors that inhibited its full expression. However, "whether the direction of genetic variation is controllable," is was what Castle sought, so when he conceded to his opponents in 1919, he lamented that "we certainly at present have to follow nature's lead rather than to lead nature, as regards the course of evolutionary change."[45]

Jennings provided a different interpretation and in effect produced a synthesis, as argued by Kingsland.[46] Those opposed to Castle were correct in arguing for the stability of the gene, but modifying factors, multiple alleles, and recombination gave natural selection a lot of power to exact its influence. He concluded, "Mendelism acts as a tremendous accelerator to the effectiveness of selection."[47] Indeed, even as the artificial induction of mutations became more feasible and productive, experimental evolutionists in later decades would generally prefer to use selection, for unlike mutation, selection is, in the words of Castle, "more controllable and its

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applying the theory to a wide variety of organisms, arguing that each experimental organism represented a broader clade. Ewing's experiment on aphids, for example, extended pure line theory to all self-fertilizing insects. Pure line theory was even applied retroactively, when the Hagedoorns compared Vilmorin wheat saved from the mid-19th century to its descendants in 1913, finding that once the pure lines had been isolated, selection had not changed the wheat in a fifty-year "selection experiment." Hagedoorn, C. and A. L. Hagedoorn, "Selection in Pure Lines," *Journal of Heredity*, 1913, 4, no. 3: 165-168.

44 "The objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies." Jennings, Herbert S., "Modifying Factors and Multiple Allelomorphs in Relation to the Results of Selection," *The American Naturalist*, 1917, 51, no. 605:301-06. Provine and Kingsland cite this passage as a sarcastic quip, but given that Jennings never truly abandoned the pure line theory - he thought genes were constant, after all - I find the passage not as clear cut as they do.

45 Castle, William E., "Piebald Rats and Selection, a Correction," *The American Naturalist*, 1919, 53, no. 627:370-76.

46 Kingsland makes this argument at the end of the "Battling Botanist."

results therefore more certain."

Thus, between 1890 and 1920, as biologists intervened upon evolutionary processes, the method by which they could control evolution shifted several times. When selection proved ineffective, the locus of control that remained was the generation of variation, as MacDougal saw, however unproductive it proved to be at the time. Ironically, as Johannsen challenged the power of selection developed their science, his followers who initially corroborated his theory, such as Pearl and Jennings, came to realize the efficiency by which it could operate. And while these two mechanisms competed, neo-Lamarckism faltered, even though some of the first experimental evolution was conducted in its name.[48] (Although I have not discussed it in my talk, eugenics is critical here, and I will be happy to discuss it in Q&A should anyone wish.)[49]

The two styles of experimental evolution I have discussed - the ecological (albeit only briefly) and the genetic - highlight a point that I think is essential to understanding the history of experimental evolution: it is not the history of the discipline of evolutionary biology. A large portion of this talk was a recasting of the history of genetics, but through the angle of the control of evolution, emphasizing that geneticists investigated more than only heredity, but also

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[47] Jennings, "Modifying Factors and Multiple Allelomorphs in Relation to the Results of Selection."

[48] This is admittedly unsatisfying, but I have yet to fully explore the experimentation of the Lamarckians.

[49] The desire to control biology almost inevitably leads to a desire to control society. I have not discussed eugenics at length in this talk partially for the sake of time, but also for the more important reason that it is so incredibly complicated — for one, it seems that eugenical views were individualistic and are not as characterizable as schools or styles. Additionally, as Diane Paul and others have shown, the correlation between a biological view and a eugenics view was not tight. The geneticists who made the discoveries in the first decade of the century that would make eugenics impossible to carry out did not articulate these arguments until well into the 1920s (specifically, Jennings and Pearl). Interestingly, Bert Theunissen claims that Hugo de Vries was skeptical of eugenics because he did not think selection was effective; furthermore, any improvements to the environment would not produce inheritable changes – but de Vries still thought these factors should be improved for the sake of the individual. See Bert Theunissen, "Knowledge Is Power: Hugo De Vries on Science, Heredity, and Social Progress," *The British Journal for the History of Science*, 1994 27: 291-311. So, while it is essential to the story, it is not yet clear to me how to navigate the influence of experimentalism upon the social views of the biologists involved. More research is required, but I would be more than happy to discuss it.

variation, mutation, and selection; effectively, the geneticists were experimenting with *evolution*.[50] As I have argued in the past, geneticists should be more readily incorporated into our standard histories of evolutionary studies, for their influence was considerable.[51]

Furthermore, Frederic Clements demonstrates that experimental evolution was not even a research program or a school of thought, for his ecological methods and goals were not at all in line with the geneticists. As Joel Hagen has shown, the experimental taxonomists put Clements' methods to work for an entirely different purpose and arrived at a theoretical position anthathema Clements' neo-Lamarckism. (I will note in passing that the experimental evolution of the 1960s is within the discipline of microbiology, a discipline that has a unclear relationship to mainstream evolutionary thought.) What unites these figures is a drive, or desire, to control the process of evolution itself. Therefore, the history of experimental evolution is not a history of a discipline, school, or research program, or even a history of a method; instead, it is a history of the drive to control evolution. Begun in the late 19th century, experimental evolution ebbed and flowed in popularity throughout the 20th century. As the methods and disciplinary home of experimental evolution shifted and transformed, always present was a desire to control evolution, and this is what I will pursue going forward.

[50] As Ernst Mayr emphasized, however, the geneticists ignored important issues such as the role of geography and ecology.

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