Journal of the History of Biology (2021) 54:403–443
https://doi.org/10.1007/s10739-021-09650-9

ORIGINAL RESEARCH

Eclipsing the *Eclipse*?: A Neo-Darwinian Historiography Revisited

Max Meulendijks[1]

Accepted: 12 August 2021 / Published online: 9 September 2021

Abstract
Julian Huxley's *eclipse of Darwinism* narrative has cast a long shadow over the historiography of evolutionary theory around the turn of the nineteenth century. It has done so by limiting who could be thought of as *Darwinian*. Peter Bowler used the eclipse to draw attention to previously understudied alternatives to Darwinism, but maintained the same flaw. In his research on the *Non-Darwinian Revolution*, he extended this problematic element even further back in time. This paper explores how late nineteenth-century neo-Darwinian conceptualizations of Darwinism were later utilized by several advocates and detractors of the Modern Synthesis. John Beatty has shown how this continuity hinges at least partly on the perceived importance of the *creativity* of natural selection. The paper provides a more thorough look at Darwin's two conflicting accounts of variation, ascribed to struggles in explaining *quantitative* versus *qualitative* characters. In doing so, it suggests that other forms of Darwinism persisted, in both the non-Darwinian revolution and eclipse periods, because of tension between *contingency* and *creativity* in Darwin's own work. This tension is traced out from Darwin's conceptions of variation into the work of Alfred Russel Wallace, Hugo de Vries, and Thomas Henry Huxley. Based on this, the eclipse narrative is criticized for not considering the meaning of Darwinism in different geographical locations. Britain and the United States showed few signs of an eclipse. Rather, the rise of German debates about Haeckel's vision of Darwinism have been mistaken for a universal decline in support.

Keywords Darwinism · Eclipse · Non-Darwinian revolution · Alfred Russel Wallace · Hugo de Vries · Thomas Henry Huxley · Evolution

✉ Max Meulendijks
Mmeulendijks01@qub.ac.uk

1 Belfast, UK

Introduction

From its inception, the very term *Modern Synthesis* was tied into its opposite—the *eclipse of Darwinism*. In this narrative, the privileged status of individual-level selection signaled the triumph of Darwinian evolutionary theory, and the combination with Mendelism made Darwinism truly scientific. For example, discussants of Darwinian medicine and psychiatry quite happily suggest that problematic past encounters between medicine and evolution could only occur before the Synthesis because the Synthesis removed problematic theories like degeneration or eugenics from evolutionary thought (Adriaens and De Block 2010, p. 135; Zampieri 2009a, pp. 333–334).

As originally conceived by Julian Huxley, and later expanded upon in the work of Peter Bowler, the eclipse has proven a sturdy historiographical construct (Huxley 1942; Bowler 1983). In advocating the term *non-Darwinian revolution*, I argue that Bowler extended this eclipse frame even further into the past. The article suggests that this eclipse framing was part of a longer "neo-Darwinian" tradition dating back to the 1880s. In doing so, this paper seeks to provide an alternative to the historiographical tradition that portrays the non-Darwinian revolution, as well as the eclipse, as problems that the Modern Synthesis solved.

Often invoked in later literature, critical scrutiny of this eclipse metaphor has gained little traction, with Mark Largent's (2009) piece most frequently cited. As Joe Cain notes, the idea of a great unified Synthesis served both its adherents, eager to associate themselves with its aura of modernization, and its detractors, eager to present themselves rebelling against the status quo (Cain 2009, p. 623). Consequently, attempts to dismiss what Ron Amundson calls *Synthesis Historiography* often fall into the same trap as what I shall characterize as neo-Darwinian historiography—they project one meaning onto Darwinian concepts where there were multiple (Amundson 2005). Both advocates and detractors, therefore, have limited the historiography of the period. This paper aims to open up the period to further scrutiny.

The paper starts with an analysis of eclipse and Synthesis frames. Uses of the eclipse narrative, from Huxley to Bowler, reveal that it tied neatly into the idea that the Synthesis was conceptually united around *creative* selection and was thus true Darwinism. Building on John Beatty's work regarding the creativity of selection, it is argued that while this conceptualization was both present in Darwin's work and in the Synthesis, neither can be reduced to it (Beatty 2016, 2019). The second section deals with the struggles between various factions of Darwinism around the turn of the twentieth century. This section introduces how different readings were possible of Darwin's work and points (as Beatty does) to a distinction between Alfred Russel Wallace and Hugo de Vries on how to understand the relation between variation and selection.

The third section builds on this distinction by showing the tension in Darwin's work between understanding variation alternatively as abundant *quantitative* variation or rare *qualitative* variation. Fleeming Jenkin's "swamping" argument is often taken to have forced Darwin to dismiss qualitative variation, but I hope to show that Darwin never quite gave up on it. The fourth section focuses on how the struggle between Alfred Russel Wallace and Hugo de Vries was marked by deciding in favor of one understanding over the other. Rather than framing this as "Darwinian" versus "mutationist," I claim that this was a debate within Darwinism. I then explore how Darwinian morphologists in the late nineteenth century, such as Thomas Henry Huxley, had preceded de Vries in thinking of evolutionarily relevant variations as rare and qualitative. The final section notes the role of geography in situating these different Darwinisms. With regard to the general eclipse narrative, it is argued that a German *eclipse of Haeckelism* is mistakenly equated to widespread issues in a transnational "Darwinism."

The Eclipse Narrative as Synthesis Historiography?

In his 1942 *Evolution: The Modern Synthesis* (hereafter abbreviated as ***ETMS***), Julian Huxley did not just coin the name of the movement of which he considered himself part; he also named the eclipse to serve as its direct opposite. Despite many novel additions, the Synthesis was Darwinian in its emphasis on "a naturalistic interpretation of evolution," as well as a willingness to use "the method of deduction" (Huxley 1942, p. 27). In his defense of deduction and naturalism, Huxley created a historical narrative still in use today.

The Synthesis supposedly enhanced Darwinism from a "non-quantitative working hypothesis" to a field akin to physics, where experiments could verify calculated predictions, such as the "omnipresence" of selection (Huxley [1945] 1947a, p. 173). While Darwin's *On the Origin of Species*, Huxley argued, had rapidly convinced biologists of the workings of Natural Selection, it lost ground in evolutionary debates between 1890 and 1915 (Huxley [1945] 1947a, p. 156). During this time, he claimed:

> Zoologists who clung to Darwinian views were looked down on by the devotees of the newer disciplines … and the *theological* and *philosophical* antipathy to Darwin's great mechanistic generalization could once more raise its head without fearing too violent a knock. (Huxley 1942, p. 25; emphasis mine)

Scientific critiques of Darwinian postulates, in other words, were accused of creating room for anti-naturalism to flourish. To overcome this, Huxley asserted, a fuller understanding of evolution had been necessary. Evolution was founded on a struggle between the nature of the organism and the requirements of the present, which had to be resolved through a new adjustment. For Huxley, this meant that Marxist dialectical materialism applied to biology—evolutionary progress required a mastery of the reconciliation between thesis and antithesis. This dialectic was both biological and social: Western, Christian, individual philosophy should similarly be brought into *synthesis* with Eastern, Marxist, collectivist philosophy (Huxley 1946, pp. 11–12, 61). To foster this process, theological and philosophical dogmas had to be removed.

Consequently, Huxley's celebration of Darwinian deduction and naturalism legitimated the use of evolutionary science to formulate an anti-religious *evolutionary humanism*. On the final page of *ETMS*, Huxley noted that there was a struggle between "the idea of a purpose directed to a future life in a supernatural world, and one directed to progress in this existing world.... [Humankind] must not continue to put off the responsibilities that are really his on to the shoulders of mythical gods or metaphysical absolutes" (Huxley 1942, p. 578). From Huxley's perspective, his grandfather, Thomas Henry Huxley, had stood up for science against religion. Between them, there had been a brief resurgence of religious and anti-scientific popularity. Now, however, in synthesizing Darwinian selection with Mendelian heredity, a more scientific and explicitly eugenic Darwinism would complete the task he believed his grandfather had laid out.

Huxley's account of the Synthesis throws doubt on Mark Largent's argument about the two reasons behind the eclipse metaphor. First, the very use of the word *eclipse*, Largent argues, suggests that the synthesis was a natural overcoming of the competing (and obscuring) theories. Indeed, Huxley's emphasis on a universally applicable dialectic method presented the progress he engendered as inevitable. Second, however, Largent notes that this narrative of discontinuity between the Synthesis and its predecessors allowed the synthesizers to distance themselves from "some problematic social and political baggage," such as eugenics and imperialism (2009, pp. 4–5). Similarly, David Depew and Bruce Weber (2011) suggest that the Modern Synthesis was accomplished by mathematization and the rejection of racism, imperialism, and eugenics. On this point is where the theory does not hold up. Most synthesizers were actively interested in eugenics. They were not, in Largent's terms, disposing of *baggage* as much as they were fighting off alternative interpretations of their own movement.

In his 1943 Romanes lecture on *Evolution and Ethics*, Huxley formulated evolutionary ethics in contrast to Nazi ethical principles, because, he explained, Nazis prioritized "tribes" at the expense of individuals, while Darwinism accepted that individuals formed "a single common but varied pool of human experience and effort" (Huxley [1943] 1947b, pp. 134–135). Similarly, in *The Growth of Biological Thought* (1982), Ernst Mayr clarified that eugenics became problematic only once applied "typologically" to groups—without regard for the individual. The early eugenicists had used unbiased and individualistic "population thinking" to "go beyond the improvements made possible by education and a rise in the standard of living" (Mayr 1982, pp. 623–624). Indeed, Raf de Bont (2010) has noted how correspondence reveals that Julian Huxley and Ernst Mayr's joint 1964 paper, which attempted to explain schizophrenia through an evolutionary perspective, was influenced by their eugenic interests.

Contrary to Largent's interpretation, then, the eclipse did not initially serve to distance the synthesizers from eugenics (although it may have been used so since). Rather, it aimed to distance them *and* the original Darwinians from undesirable theological and collectivist interpretations of evolutionary ethics. Several synthesizers associated "scientific" eugenics with Huxley's humanism rather than contemporary alternatives. Later accounts of the Synthesis sometimes conflate the two and assume eugenics amongst the unscientific ideologies surpassed by the

Synthesis (Zampieri 2009a; Largent 2009; Adriaens and De Block 2010; Depew and Weber 2011).[1]

The view that extra-scientific goals were crucial is further cemented by Huxley's lackluster historical account of the *scientific* eclipse, which ostensibly gives the chapter "The Eclipse of Darwinism" its title (1942, pp. 22–28). In this account, the statistical biometricians were the "true-blue Darwinian stream," whose ideas eventually merged with those of their Mendelian opponents to give rise to a revitalized Darwinism (Huxley 1942, p. 24). Although *ETMS* comprehensively detailed contemporary research, the history consists of debates between mostly British actors from a limited set of disciplines. Mayr would similarly come to emphasize a growing divide in biology between Mendelian experimentalists and naturalists but saw no need to go into detail (see especially Mayr 1982, pp. 540–570). After all, these complaints had been overcome by the Synthesis.

The *scientific* conceptualization of the eclipse was significantly expanded on by Peter Bowler in his *The Eclipse of Darwinism* (1983). As an account of the state of Darwinism in the late nineteenth and early twentieth centuries, it dealt extensively with the competing theoretical alternatives present at the time. Huxley's eclipse provided Bowler with a snappy title as well as the support of an authoritative figure for his narrative.[2] In addition, however, two explicit motives for Bowler's interest in the eclipse narrative are admitted in the book.

First, if Huxley's eclipse had been an *attack* on theological and philosophical alternatives, Bowler's was a *defense*. Religious and secular detractors, Bowler noted, commonly sketched an image of Darwinism as a dogma that scientists had never bothered to expose to scrutiny (1983, p. 5). In contrast, the eclipse narrative suggested a shift—from the early popularity of Darwinism, despite its perceived problems, to the rising disinterest around 1900 without significant new theoretical challenges (Bowler 1983, p. 12). Second, and perhaps more importantly, Bowler used the eclipse narrative to justify research on non- or anti-Darwinian alternatives and understand their importance to the intellectual climate of the time. As indicated in later work, previous researchers had shown "more about how Darwin responded to objections than about the objections themselves" (Bowler 1988, p. 91).

Bowler's further study of alternatives to Darwinism changed his attitude to the notion of the eclipse. The 1992 paperback version of *The Eclipse of Darwinism* is prefaced by the claim that technically there may not have been an eclipse, because "*Darwinism*—in the modern sense of that term—had never been very popular" (Bowler 1992, p. x). In *The Non-Darwinian Revolution* (1988), Bowler suggested that Darwin did not convince scientists to accept his theory of natural selection. Rather, he had convinced "Darwinians" to rally around an evolutionary science, without committing to a specific view on mechanism (Bowler 1983, p. 28; Bowler

[1] In the case of Zampieri, Adriaens, and De Block, it is only indirectly stated. Zampieri used Mayr's work to argue that that modern applications of Darwinism to medicine cannot be eugenic due to their populational approach—unlike pre-Synthesis typological traditions. Adriaens and De Block similarly associated eugenics with degeneration theory and argue that the Synthesis vanquished degenerationism.

[2] In comments on a previous draft of this paper, Peter Bowler confirmed these implicit reasons.

1988, pp. 66–71). Darwin's *Origin of Species* (1859) had provided fertile ground for evolutionism, but not Darwinism. Hence, more attention was required for "non-Darwinian" ideas before historians could understand engagement with evolution in the latter half of the nineteenth century.

The Non-Darwinian Revolution undermines *The Eclipse of Darwinism*, however, by essentially denying the shift in popularity. Instead of a temporary upsurge of *anti-Darwinism* around 1900, the *Origin* had had an immediate *non-Darwinian* response. Effectively, the eclipse narrative was brought back in time to 1859. As Bowler claims in a more recent re-evaluation of the eclipse narrative, the success of natural selection "required a second revolution … which in science was associated with the emergence of Mendelian genetics" (Bowler 2005, p. 22). If anything, then, the *Non-Darwinian Revolution* strengthened Bowler's ties to Huxley's narrative. Darwinism was again presented as a "naturalistic" view of natural selection, which had largely been ignored by his followers until it finally culminated in a conceptual synthesis.

By clinging to Huxley's narrative, a problematic role for the Synthesis is maintained. I agree with Amundson that it was unproductive for Bowler's work to frame certain alternative conceptions as "flawed theories that preceded our modern scientific understanding" rather than "legitimate and productive attempts to solve problems" (Amundson 2005, p. 107). I am not as confident as Amundson, however, in characterizing Bowler as contributing to "the Synthesis interpretation of history" (2005, p. 12).[3] In fact, I am not sure if Huxley and Mayr were really contributing to a common *Synthesis Historiography* if that consolidates them as representatives for the entire project.

Regarding the Synthesis, Jean Gayon distinguished between several conceptions. In terms of theory, it is often referred to as a neo-Darwinist consensus on the *genetic theory of natural selection* (Gayon 1990, pp. 3–4). In that case, the synthetic theory is "the monotonous claim" that natural selection is the main factor in evolution, which acts upon variation in Mendelian genetical terms (Gayon and Huneman 2019, p. 532). Institutionally, it can refer to the rise of *Evolutionary Biology* as an organized discipline from the 1940s onward, with its own journal, societies, etc. Joe Cain has written extensively on the way Synthesis architects in the 1930s and 1940s attempted to legitimize biology as an autonomous discipline worth funding, whose work should not be reduced to the methods of physics or chemistry (Cain 1993). Similarly, Smocovitis analyzed how these struggles for authority led to Charles Darwin's reinvention as a disciplinary founding father—the "Newton" of Evolutionary Biology (Smocovitis 1992, p. 56). Gayon and Huneman suggest further that the evolutionary synthesis can be conceived as an intermediate between theory and institution—a flexible research program that aimed to empirically prove that selection was in the main force responsible for evolution but allowed for alternative explanations in specific instances (2019, p. 532).

The problematic nature of portraying the Synthesis as a conceptual consensus on Darwinism can be illustrated by the fact that the unifying narrative hid noticeable

[3] Especially in light of Bowler's later work, for instance, Bowler (2013, 2017).

disagreements. Richard Delisle noted various incongruences, such as Mayr's insistence that evolution was a biological phenomenon in contrast to Theodosius Dobzhansky and Bernhard Rensch's conceptions of the biological as an element of wider cosmic evolution (Delisle 2009). If William Provine's early work had suggested that the rise of population genetics corresponded roughly with the Synthesis, he later indicated that the Synthesis should be considered an "evolutionary constriction" (Provine 2001, pp. 197–205). Although there had been agreement that certain disciplinary traditions should be cut out, "there were about as many different versions of the evolutionary synthesis as there were major evolutionary biologists associated with it…. Each felt his contribution to the synthesis was slighted and that he had to fight for his proper place" (Provine 1992, p. 169).

Nevertheless, in *The Evolutionary Synthesis* (1980), Mayr argued that the project had produced conceptual consensus over the role of gradual evolution, natural selection, and genetics in the field of evolutionary biology (p. 1). He acknowledged that the exact process of synthesis could be seen from different perspectives by those in different disciplines, countries, and even locations within the same country. This acknowledgment of geographical difference, however, did not preclude a universalist grand narrative. The Synthesis had been less about "the discovery of new facts" than "the removal of misunderstandings," which served merely as the "final implementation of the Darwinian revolution" (Mayr 1980, p. 43). The claim to be the "final implementation" suggests the Synthesis put an end to the debate on what Darwinism actually entailed.

Following a similar conception, Stephen Jay Gould attacked the Evolutionary Synthesis for clinging tightly to a belief that evolution was about adaptation, which provided little room for studying the constraints of an organism's organization (Gould 1980, pp. 128–129). In a defense of the Synthesis, G. Ledyard Stebbins and Francisco Ayala claimed that "selectionist" and "neutralist" accounts of evolution were both valid within its population genetics framework (Stebbins and Ayala 1981, p. 967). In support of this, Steven Orzack suggested that Gould mistakenly took Mayr's (and Ronald Aylmer Fisher's) strong support for natural selection as representative of the Synthesis instead of recognizing its pluralism (Orzack 1981).[4] Gould would later come to acknowledge that there had been pluralism initially, but he argued that the Synthesis had "hardened" over time as selectionism came to predominate (Gould 1983). Niles Eldridge's *Unfinished Synthesis* (1985) similarly harkened back to the early Synthesis to advocate a reintroduction of its plurality, whether with regard to multiple levels of selection or the focus on spatial and temporal species discontinuity. Indeed, Delisle reminded us that pluralism persisted more readily than was rhetorically suggested, but historically this rhetoric matters (Delisle 2017). Orzack's answer to Gould leaves out how the narrated triumph of adaptationism and selectionism over non-adaptive alternatives played a key role in the justification of the Synthesis by architects such as Huxley and Mayr.

Cain suggested that conceiving of a coherent modernizing Synthesis proved useful for its adherents but equally so for critics seeking "David and Goliath"

[4] Most of all, he emphasized the enduring legacy of Sewall Wright.

narratives (Cain 2009, p. 623). Indeed, Gould framed Darwinism simplistically and claimed that his own pluralist Darwinism "violates directly the fundamental reductionist tradition embodied in Darwin's focus on organisms as units of selection" (Gould 1982, p. 386). In addition, Gould argued that the *creativity* of natural selection should be considered the focus of Darwinism (Gould 2002). Following Gould, Arlin Stoltzfus and Kele Cable argued that mutationist-Mendelian critiques correctly attacked incorrect Darwinian ideas by disputing that creativity (Stoltzfus and Cable 2014). John Beatty (2016, 2019) suggested this creativity hinged on the idea that selection initiated change—it was not a two-step process (variation first and selection after), because selection always appeared to have the right variations available. In a more nuanced point, he argued that mutationists upheld the two-step process, while Darwinians often did not.

Could Darwinism be reduced to such reductionism? Beatty notes that the mutationists claimed to be siding with Darwin on the *chance* nature of variations, but he argues that Darwin had eventually committed himself to the *creative* process, like some of his followers (Beatty 2016). I think, however, that Darwin's indecision was not resolved that easily. In this regard, Delisle helpfully differentiates between Darwin's rhetoric, which occasionally presented his theory as a "neat, compact, and abstract theoretical construct," and the actual "extreme pluralism" illustrated in the *Origin* (Delisle 2017, p. 147). David Depew has commented on how Darwin refuted, reformulated, or co-opted alternative explanations like use-inheritance or orthogenesis and how this strategy was continued by his followers (Depew 2017, p. 63). As Helen Liepman and Thierry Hoquet have pointed out, that initial pluralism in the *Origin* only became more pronounced as Darwin made numerous changes over the course of its six editions (Liepman 1981; Hoquet 2013). It can be said that Darwin never settled on a single, exclusive definition of Darwinism, nor did he establish clear boundaries.

Consequently, James Moore has noted how the quest for who "correctly" understood Darwinism is historiographically questionable, as shown by the *historical* contestations around the meaning of that term (Moore 1991, p. 358; see also Hale 2015). In other words, we must accept that Darwinism has never been united or encompassing. In a later edition of *The Evolutionary Synthesis*, even Mayr would come to argue that in 1947 "everyone thought the synthesis of the two camps had been completed … however, this was not the case. For the reductionist geneticists, the unit of selection was the gene, whereas the naturalist insisted it was the individual" (Mayr 1998, p. xiii). There can be multiple forms of Darwinism, which could be interacting or dividing along a variety of faultlines. Evolutionists like Gould, Delisle continues, must be careful not to take the rhetoric for granted and to accept that their own pluralism echoes that of Darwin, the Synthesis, and elsewhere. Delisle's proposed solution to the ensuing looseness in the application of "Darwinism" is to abandon the term. In this view, Darwin's name was not truly popularized until the Evolutionary Synthesis and often given only lip service. Echoing Moore's issues with the historiography of Darwinism, Deslisle argues that this approach would do away with:

> [the] task of weighting "good" and "bad" research programs with a scale evaluating Darwinian purity. It also eliminates the witch hunt for epithets like "ultra-darwinians," "near-darwinians," "pseudo-darwinians," or "anti-darwinians." Darwinism cannot simply be equated with natural selection. Since there is much more to the *Origin of Species* than the theory of natural selection … why should Darwin's name be exclusively associated with natural selection. (Delisle 2017, p. 147)

It can be agreed that Darwinism was more than natural selection and that it should not be up to the historian to unleash "witch hunts" for those deviating from "Darwinian purity." Is that, however, sufficient ground to abandon the term Darwinism or its epithets? As Diarmid Finnegan has noted, even if we should not aim to study the perseverance of a singular idea, we can still trace "the illimitable ways in which threads from the fabric of Darwin's thought were picked up and re-worked by others then and now" (Finnegan 2010, p. 261). The epithets tell us much about the different streams of Darwinian thought—even before the Synthesis—both about how each stream sought to justify what threads were picked up, as well as how those threads were reworked.

To engage in this kind of study requires us to move away from any *essentialist* definition of Darwinism. David Hull suggested that one way to do this for the Darwinian revolution was through a sociological approach (Hull 1985). By emphasizing the Darwinians as a social group, studies could accept the conceptual and disciplinary heterogeneity among its constituents because social ties to Darwin bound them together as a community willing to defend and support his research program (Hull 1985, pp. 785, 796). Coordination among T.H. Huxley, John Tyndall, and other members of the anti-clerical X club—a dining club of select scientists that met monthly—played a firm role in this regard (see especially Barton 2018). This approach appears a useful tool for framing the Darwinian revolution because Darwin can serve as the final arbiter over whether an individual was conceptually close enough to be considered a Darwinian. However, such an approach is only feasible if we limit ourselves to when Darwin himself was alive. As Darwin entered historical time, so faded the advantage of having him as the arbiter of who was part of *the* Darwinian social group. If our study is to include the eclipse period, a different non-essentialist approach is required.[5]

Consequently, it makes more sense to continue from the early 1880s with a conceptual approach to Darwinism, as long as that can do justice to the variety of perspectives under (and contestations over) the designation. In her discussion of the 1909 Darwin celebration, Marsha Richmond observed how participants followed a similar strategy (Richmond 2006, p. 465). They first established legitimacy by invoking Darwin's work as the inspiration for their own, then introduced factors and

[5] Another way Hull attempted to get around the issue of *essence* was by emphasizing *lineage*—to follow the evolution of a theory from person to person over time. As Jacques Roger pointed out, however, cultural ideas are often hybrids of distant notions, not to mention that a theory can be borne of many parents (Roger 1985). Similarly, I would argue, immense changes in conceptual understanding can take place over the course of an individual's work. Hence, lineage does not seem appropriate.

interpretations based on their own disciplinary/cultural background. Finally, they showed how these new factors improved upon Darwin while maintaining compatibility. The deference paid to Darwin is undoubtedly an important influence on the progression of evolutionary thought (for good or ill) and must be acknowledged. I refer to this two-step process of *improving* upon Darwin, but also maintaining *compatibility*, as *Darwinization*. I hope to show that conceptual tensions in Darwin's work could not be resolved by his followers without deciding to exclude alternative (though valid) interpretations.

Here Darwin himself can serve as a (light-touch) metaphor. Despite being named *On the Origins of Species*, his book threw doubt on whether *species*, as understood at the time, actually existed. Instead, it drew attention to factors at the individual and variety level as being more crucial than strictly the species designation. Similarly, historical studies of conceptual "Darwinism" must recognize that the term is highly unstable (as Darwin's work was not without its internal contradictions), and different interpretations might arise within an individual's work or between individuals. Nevertheless, recognizable varieties might show a relative stability at certain times and in specific places. Moreover, reformulations to increase Darwinism's workability might have removed elements that Darwin himself would have considered crucial.

A description of conceptual Darwinism must acknowledge that Darwinists, if they wished to do more than merely copy and paste Darwin's work, necessarily needed to move beyond Darwin's own views to fit new circumstances. This understanding will help us counter the belief that the eclipse period saw only one Darwinism—besieged on all sides. First, we must come to grips with the start of the narrative that placed *creative* selection at the heart of Darwinism: the conception of a "pure" Darwinism.

Neo-Darwinism: Defending the "Purity" of Darwinism

What is neo-Darwinism? Ernst Mayr noted that neo-Darwinism "was coined by [George] Romanes in 1895 as a designation of Weismann's theory" (Mayr 1984, p. 146). Reif, Junker and Hossfeld took Romanes's 1895 claim as the basis as well, but noted that it designated an exclusive emphasis on natural selection by Weismann and Wallace (Reif et al. 2000, p. 43). In both cases, they deny the relevance of the term for the Modern Synthesis. What such approaches miss out on, however, is the *historical* correction that Romanes's epithet implies. To draw out its significance, we will first need to discuss the term *pure Darwinism*, to which Romanes's term was a response. To do so, we will have to start in the 1870s, when a formerly Darwinian zoologist, St. George Jackson Mivart (1827–1900), formulated a particular characterization of Darwinism.

In his *The Genesis of Species* (1871), Mivart launched an attack on what he considered "the pure Darwinian position," which emphasized only natural selection working on small "chance" variations (Mivart 1871, pp. 20, 67). James Moore gives an excellent account of how Darwin indirectly defended the theory of natural selection by seeking the publication of Chauncey Wright's pamphlet on "Darwinism" (Moore 1991). Wright defended Darwinism, but similarly associated it with (and hence helped popularize) its association with the exclusive power of natural selection. What this reading leaves out, however, was Darwin's more direct response to Mivart's attack.

Both publicly and privately, Darwin recoiled at such a limited characterization of his theory. To Alfred Russel Wallace, Darwin wrote that Mivart's criticism had been unfair because he had quoted selectively and ignored Darwin's writings on use inheritance (Marchant 1916, p. 258). In the sixth edition of the *Origin* (1872a), Darwin not only defended natural selection but also noted that he always had "highly" valued use inheritance and had elaborated on them in *Variation under Domestication* "at greater length than, I believe, any other writer" (Darwin 1872a, p. 187). That he had ever held natural selection as an exclusive means of evolution, without regard for other factors, appeared to him a strawman. In his "Mr. Darwin's Critics," Huxley similarly could not agree with Mivart's characterization of Darwinism. If the "absolute and pure Darwinian" was to hold the ideals attributed to them, Huxley asserted, then "I doubt if I can ever have seen one alive" ([1871] 1893a, p. 474). Darwin had hardly been dogmatic on the issues of natural selection and variation and had become less so over time (Huxley [1871] 1893a, p. 475).

It was not until 1888 that Darwinian zoologist Edwin Ray Lankester (1847–1929) revived the term *pure Darwinism* in his article on "Zoology" for the *Encyclopedia Brittanica*. The purpose, it will be no surprise, was quite the opposite to Mivart's. Here, Lankester emphasized that Darwin never admitted the *necessity* of the inheritance of acquired characters and thought it was relevant only in some cases (Lankester [1888] 1890, pp. 372–374). Thanks to August , Lankester continued, it was likely that evolution could be explained by "pure Darwinism and be entirely dissociated from the Lamarckian heresy" ([1888] 1890, pp. 374–375). He reasserted exclusive explanatory power of "what may be called 'pure' Darwinism" in a letter to *Nature* (Lankester 1888, p. 364).

In that same journal, Darwinian entomologist Edward Bagnall Poulton (1856–1943) attacked Romanes's interest in the inheritance of acquired characters in relation to defensive coloring (Poulton 1888a, p. 296). Having been Darwin's research assistant for many years, Romanes noted his support for "*what [Poulton] calls* the Lamarckian conception" (Romanes 1888a, p. 364; emphasis mine). In response, Poulton noted Lankester's dichotomy (Poulton 1888b). Similarly, Darwinian entomologist Raphael Meldola (1849–1915) insisted that the "purely Darwinian stand-point" could explain protective coloring in a way the "new Lamarckian school" could not (Meldola 1888, p. 388). Romanes complained of being branded a Lamarckian and argued it paradoxical that the "purer" Darwinism was supposedly made, the further it seemed to stray from the *Origin of Species* (Romanes 1888b). Consequently, "the school of may properly be called Neo-Darwinian; pure Darwinian it is certainly not" (Romanes 1888b, p. 413; see also 1888c, p. 173). Here, Romanes revived the term *Neo-Darwinian*—previously used by Samuel Butler.[6] Now the term denoted how the pure Darwinians were not moving towards an

[6] The first use of the term *neo-Darwinism* appeared in Samuel Butler's *Unconcious Memory* in 1880. Butler argued that Erasmus Darwin's theory of evolution, based on the inheritance of acquired characters and animal volition, should be considered the original Darwinism. Neo-Darwinism emphasized natural selection instead. Interestingly, Butler specifically credited Wallace with first placing "natural selection" in opposition to Lamarck's inheritance of acquired characters in a general sense, while Darwin's refuta-

improved version of Darwin's position but were actually deviating from its comprehensiveness in attempting to "out-Darwin Darwin" (Romanes 1887, p. 402).

In an 1889 letter to Francis Darwin, Romanes complained that "Wallace's jealousy of natural selection" and his consequent rejection of sexual selection was "forcing it into explanations which are plainly false" (Romanes [1889] 1896, p. 210). He argued that Lankester's pure Darwinians were similarly damaging natural selection. That same year, Poulton's translation of Weismann's *Essays upon Heredity* (Weismann 1889) as well as Alfred Russel Wallace's *Darwinism* (Wallace 1889) were published. Over 1888 and 1889, the two had been in regular correspondence. Wallace supplied Poulton with chapter drafts to review and, in return, received Poulton's translated excerpts of Weismann's work to incorporate.[7]

In the preface to *Darwinism*, Wallace, the co-discoverer of natural selection, argued that Darwin had unduly receded from his position in *Origin* due to later critiques. In rejecting use inheritance and sexual selection, Wallace argued, the main Darwinian doctrine of natural selection could be re-emphasized to create "pure Darwinism" (Wallace 1889, p. viii). August Weismann's contributions on the non-transmissibility of acquired characters cemented the role that natural selection could play as a universal presence in organic change and gave it a reach "even Darwin hesitated to claim for it" (Wallace 1889, p. 444).[8] The Darwinization of biology, then, entailed in Wallace's eyes the ever enhancing of natural selection's reach and efficacy in biological explanations. By this logic, even Darwin had failed to do so after his initial contribution. In this portrayal of Darwinism, we find a nascent eclipse narrative among the self-proclaimed "pure Darwinians." The first edition of *Origin* had given the signal to natural selection, but later work had not increased its explanatory power. His self-appointed successors would now finish the job.

In his 1896 biography of Charles Darwin, Poulton continued to write this conception into history. The Darwin-Wallace joint memoir of 1858, he noted, had seen Wallace explicitly contrast his views with Lamarck's. Consequently, it should be remembered that "this contrast, which has been so often drawn, was therefore originally contained in the first public statement of natural selection" (Poulton 1896, p. 79). The same fact had led Romanes to suggest calling the exclusive action of natural selection "Wallaceism" instead (Romanes 1889, p. 152). Darwinism should be used "as Wallace uses it," Poulton argued, to exclude causes that did not originate with Darwin. Otherwise, damage to these causes could damage the integrity of Darwinism, which would be "most unfair to the memory of Darwin" (Poulton 1896, p. 99).

Footnote 6 (continued)

tions had been less resolute (Butler 1880, pp. 281–283). Romanes produced scathing reviews of *Unconscious Memory*, with special attention to the suspicion thrown upon Darwin's conduct (Romanes 1881a, b; see also Pauly 1982).

[7] Alfred Russel Wallace to Edward Bagnall Poulton, 18 Febuary 1889, Wallace Letters Online, accessed on 17 February 2021, https://www.nhm.ac.uk/research-curation/scientific-resources/collections/library-collections/wallace-letters-online/4362/4595/T/details.html. Original held at Hope Entomological Library, Oxford University Museum of Natural History, with finding number ARW15.

[8] Weismann had named this the 'Allmacht' (often translated as all-sufficiency) of natural selection.

The commonality that Romanes identified was not the neo-Darwinian denial of use inheritance but an ideal of the purification of Darwinism that seemed fundamentally opposed to Darwin's own approach. It was an attempt to rewrite history through "steady misrepresentation" (Romanes 1888c, p. 173; Darwin 1872a, p. 421). Had Darwin not responded to Mivart in the sixth edition of the *Origin* (1872a) and clarified that an exclusive emphasis on natural selection had never been his position? Neo-Darwinian claims relied on "inversions of the truth" that failed to see that Darwin's research program studied the role of natural selection among various other factors (Romanes 1895, p. 12).

The new century started with a new pretender to Darwin's legacy. In two large volumes (1901, 1903), the Dutch botanist Hugo de Vries (1848–1935) laid out his mutation theory, which he positioned against Wallace's interpretation of selection. If Darwin's selection theory had been built on "hosts of doubts" regarding selection and variation, Wallace's was clear and precise—to its detriment (de Vries 1901, p. 40). Throughout the work, de Vries criticized Wallace's selection theory for supporting "individual differences" over "single variations," while he kept Darwin in the clear. Dutch embryologist Ambrosius Hubrecht (1853–1915) supported this interpretation. If Darwin and Wallace had initially formulated the same principle, Darwin had remained mired in "philosophic indecision," but Wallace had decided in favour of an incorrect interpretation of variation (Hubrecht 1904, pp. 208–213). He argued that de Vries, "far from having undermined Darwin's Darwinism … has completed, purified and simplified it. To Wallace's Darwinism, however, de Vries has dealt a severe blow" (Hubrecht 1904, p. 212). Another "pure" Darwinism had arisen.

The American geneticist George Harrison Shull (1874–1954) asserted that while neo-Darwinians had been quick to attack the mutation theory for denying individual differences, de Vries illustrated how mutations were a logical outgrowth of Darwin's thinking on variation (Shull 1905, p. 90). In the *Contemporary Review*, Wallace attacked mutationists for seeking to place "saltations" over "the slower process of variation and selection as maintained by Darwin" (Wallace 1908a, p. 133). Hubrecht reiterated that they had only attacked "Wallaceism," and mutationism had been "grafted" onto the "very healthy plant of Darwinism" (Hubrecht 1908, p. 629). In turn, Wallace heavily objected to what he characterized as Hubrecht's bold allegation of there ever having been differences in opinion between Darwin and himself (Wallace 1908b, p. 716). Poulton spoke appreciatively of the support for Darwin by de Vries and Hubrecht, but argued that Darwin had never supported single variations (Poulton 1909, p. xii).

Romanes's neo-Darwinian definition is of use to our general critique of neo-Darwinian historiography as well. Bowler insisted that Gould's "hardening" of the Synthesis around adaptationism meant "Darwin's view of evolution thus enjoyed a belated triumph" (Bowler 1988, p. 129). Similarly, Gould's own account of the creativity of natural selection noted that de Vries held a "manifestly un-Darwinian view" and attributed his attempts to claim the Darwinian mantle away from Wallace to the psychological hold of his hero worship (Gould 2002, p. 439). We must appreciate, however, how this explanation privileges the neo-Darwinian account of Darwin's views. Instead, we must recognize that Darwin wavered between *quantitative* and *qualitative* differences, and between the *creativity* and *contingency* of selection. One way to emphasize this is to acknowledge the two different ways in which Darwin conceived of variation. The following section provides a brief overview of Darwin's conceptualizations of variation, after which the distinct Darwinisms of Wallace and de Vries will be reassessed.

Selection and Variation: The Role of *Creativity* and *Contingency*

Darwin's Concepts of Variation

It is well known that Darwin emphasized the link between artificial selection used in breeding and the important role of natural selection in nature.[9] Already in the first edition of *Origin*, however, Darwin's treatment of variation seems to conflict with his account of selection. While he confidently noted that natural selection can accumulate differences "in any given direction," he also asserted that "unless profitable variations do occur, natural selection can do nothing" (Darwin 1859, pp. 45, 82). Although this tension is noted by Beatty, I do not think it is realized quite how deep it goes (Beatty 2016). Further exploration of this tension between Darwin's selection and variation prepares us for a greater appreciation of the discussions of Wallace's neo-Darwinism and de Vries's mutationism.

In Darwin's theory, variation was an independent factor that he embellished with the theory of pangenesis presented in *Variation of Animals and Plants Under Domestication* (1868a, b). Using the metaphor of budding, Darwin suggested that developing cells would throw off "gemmules"—small elements which contained the hereditary information and circulated freely through the organism (Darwin 1868b, p. 374). Gemmules could divide like cells and turn into similar cells as those from which they were derived. Gemmules would be produced throughout an organism's lifetime and collected in buds or "sexual elements" (p. 377). Some gemmules may lay dormant for several generations, even after fertilization (p. 384).

Heritable variability could be explained on two grounds. First, the prominence of a trait in offspring could be determined by the relative number and vigor of parental gemmules for each trait. Discrepancies in quantities and vigor between parental gemmules explained why some traits appeared to take only or more after one parent, while others showed an even blending of characters. These quantitative discrepancies accounted for "much fluctuating variability" (Darwin 1868b, p. 396). Second, changed conditions or use of parts could modify parental cells and hence also the gemmules themselves, which would then develop "into new and changed structures" (p. 397; see also Darden 1976).

Rasmus Winther has shown most comprehensively that Darwin consistently believed variation to be *induced* by external influences, although the internal

[9] Bowler and Gayon had even claimed that this emphasis put Darwin apart from Wallace, who appeared initially more concerned with variety-level selection and explicitly distanced himself from likening research on domestic species to those of the wild environment (Bowler 1976; Gayon 1998).

constitution would *shape* the nature of variation (Winther 2000). Similar constitutions under similar conditions could thus lead to similar variations. Darwin's emphasis on internal structure, I would argue, married the concepts of variation and common descent. For example, he suggested that species were unlikely to vary in characters they had in common with closely related species—which he named *generic* characters—as these had been stabilized by long-continued selection. In contrast, characters in which a species had varied from a common ancestor—its *specific* characters—would continue their tendency to vary (Darwin 1859, pp. 154–158, 474).

In addition, *analogous variation* would come to play an increasing role in Darwin's study of variation and advocacy for common descent. This kind of variation was only briefly touched upon in the first edition, where he argued that distinct turnip and pigeon species appeared to show similar variations due to the "*vera causa* of community of descent," although the changes induced were not structurally important (Darwin 1859, pp. 159, 169). By *Variation under Domestication* (1868a, b), the role ascribed to analogous variation had expanded from pigeons and turnips to other fowl and plants. Darwin noted that peaches and nectarines had varieties of similar colors, such as yellow, red, and white. These resemblances could not be due to each colored nectarine variety having evolved separately from their similarly colored peach ancestors; it was equally unlikely that selective pressures had induced the similarities. Instead, the common constitutions of both species had induced similar variations (Darwin 1868b, pp. 348–352).

In the sixth edition of *Origin* (1872a), Darwin went still further by using analogous variation to explain electric organs in fish and luminous organs in insects. These organs appeared in distantly related species and differed significantly in how they were constructed and where they were situated in the body (pp. 151–152). Hence, they could not have been inherited from a common ancestor. Nevertheless, Darwin argued, these species would have inherited "so much in common in their constitution" that similar conditions of life would have produced similar variation (1872a, p. 375). Analogous variations would thus increase the *chance* of electric variations in even distantly related fish species and of luminous variations in related insects. However, these common variations could not bring about any substantial structure unless natural selection could shape the variations into functional electric and luminary organs fitted to the overall structure of each species.

It is noticeable that Darwin's examples for analogous variation were largely *qualitative* differences (novel traits such as distinct coloring) rather than *quantitative* (intensity of traits like shades of the same color). Bowler observed that Darwin inconsistently switched between two understandings of variation (Bowler 1974, p. 197; see also Gayon 1998, pp. 99, 401). First, Darwin often described "individual differences," whereby individuals can exhibit a trait in all gradations within a continuous range. No two people are exactly alike, but neither do they stand out from the population. Differential fertility in favor of one side of the range over another would slowly shift the mean of the population in that direction. Second, Darwin spoke of small variations that have a single origin, which produce a quality in the individual that other individuals do not have. They are comparatively rare, which explains Darwin's emphasis on favorable variation being more likely in large populations or requiring a long time to appear (Bowler 1974, pp. 206–207). These were different from "sports," which (as sizeable single variations) would disrupt the alignment between the individual and the environment. As Gayon summarized, Darwin sometimes perceived selection as the *displacement* of a population mean and sometimes as the *diffusion* of a trait in a population (Gayon 1998, p. 401).

Both Bowler and Beatty draw attention to two related examples of wolves that Darwin used to illustrate how natural selection would work with variations (Bowler 1974; Beatty 2010, 2016). On the one hand, he claimed that if easily caught prey decreases in number relative to more difficult prey, the swifter wolves would have a larger chance of surviving than slower wolves and would hence be "selected" (Darwin 1859, p. 90). The entire population shifts continuously in a direction because the wolves at the swifter end of the range outlive (or outbreed) wolves on the slower end. On the other hand, he noted how an advantage that benefits an "individual wolf," such as a slight tendency to catch different prey could be inherited by its offspring. Eventually, the distinction might create a variety that could "either supplant or coexist with the parent-form of wolf" (Darwin 1859, p. 91).[10] They eventually form a variety because a new *quality* has been introduced, even if only small. Within the population, wolves either have the (slight) change in dietary preference or maintain the original preference.

In the *Origin's* fifth edition (1869), Darwin replaced the second example with an acknowledgment of an 1867 critique by Fleeming Jenkin (1833–1885), professor of engineering at Edinburgh University. Beatty and Bowler take Darwin's reaction to signify a simplification of his theory to an exclusive, range notion of variation.[11]This seems to fit with his 1869 admission to Wallace that Jenkin had convinced him that individual differences are more important than single variations.[12] However, by engaging with Jenkin's work, we can see that Darwin persisted more than is sometimes suggested. Jenkin categorized his critique under five headings, of which "Variability," the "Efficiency of Natural Selection," and "Lapse of Time," are briefly worth summarizing.

On variability, Jenkin compared the range of variations within a species to a sphere. Although variation would be prevalent in all directions around the mean or center of the sphere, it would diminish the further an individual was removed from the mean of a population towards the edge of the sphere. Jenkin criticized Darwin

[10] The group was a significant unit of analysis in Darwin's thought. Indeed, on several occasions, Darwin appears to suggest that the struggle between varieties of the same species is "almost equally severe" to that of individuals of the same species (Darwin 1859, p. 75). There was no advantage to individual organisms being less fertile when crossed with other varieties, nor could selection work if it failed to "give any advantage to its nearest relatives or to any other individuals of the same variety" (Darwin 1866, p. 312). In *The Descent of Man* (1871), Darwin noted that even traits that would promote self-sacrifice, and might thus benefit groups rather than individuals, "would be natural selection" (Darwin 1871, p. 160).

[11] Similarly, Kyung-Man Kim suggests that Darwin's emphasis on continuous variation would have spared him Jenkin's critique, but "unfortunately, however, Darwin sometimes wrote as though even *small* favourable variations occurred in *rare* individuals" (1994, p. 42; emphasis mine).

[12] To Alfred Russel Wallace. 2 February [1869]. Darwin Correspondence Project, "Letter no. 6591," accessed on 13 January 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-6591.xml

for suggesting that reversion to the mean could be selected against—as offspring that experienced reversion lost out against offspring that continued to diverge—without providing experimental proof (Darwin 1859, p. 154; Jenkin 1867, p. 283).

Regarding the efficiency of natural selection, Jenkin distinguished between common variability due to individual differences and the rare variability that resulted from individual "sports" (Jenkin 1867, pp. 286–287). Were there no limits on variation, the range concept could no doubt improve or diminish "every useful organ of their ancestors" to be more in line with the environment, but it could not lead to the appearance of novelties (Jenkin 1867, pp. 287–288). If enough individuals on one side of the mean value survived, and those on the other side did not, quantitative change would be engendered in the population. In contrast, sports could lead to novelties, but these would appear only in rare individuals. Under the assumption of blending, modifications or advantages of any size would eventually be "swamped by numbers," as every crossing with non-sporting individuals would halve the variation until it eventually disappeared (Jenkin 1867, p. 294).[13] Based on Lord Kelvin's calculation of the age of the earth, Jenkin noted there would not be enough time for this type of variation to work, even if slow progress could be made.[14]

Darwin's replacement of the individual wolf example by an acknowledgment of the swamping problem is not the full story of Darwin's response to Jenkin. We will ignore the Lamarckian possibilities of pangenesis because, while the 1868 introduction fits in terms of timing, Geison observed that the theory had already been drafted before the confrontations with Fleeming Jenkin (and Lord Kelvin), so it had not been designed to speed up evolution or to defeat swamping (Geison 1969; Jenkin 1867, pp. 380–384).[15] Rather, I wish to focus on how Darwin persisted that varieties could have single origins, even if a variation was swamped. As he wrote to his friend Charles Kingsley regarding Jenkin's article:

> Sudden sports … I have always thought, but now more clearly see, would generally be lost by crossing. [The reviewer] does not however notice, that *any variation would be more likely to recur in crossed offspring still exposed to same conditions*, as those which first caused the parent to vary."[16]

[13] Interestingly, Jenkin notes a solution to the problem that Darwin overlooked: "A Darwinian may … contend that the offspring of 'sports' is not intermediate between the new sport and the old species; he may say that a great number of the offspring will retain in full vigour the peculiarity constituting the favourable sport. Darwin seems with hesitation to make some such claim as this" (Jenkin 1867, p. 291).

[14] Over the course of the 1860s, Kelvin published several articles which calculated the age of the earth as likely only 100,000,000 years old. Susan Morris notes how it was Jenkin's argument that drew Darwin's attention to the limited time this posed for his theory (1994, p. 342).

[15] Although Darwin himself thought pangenesis was one of the few theories that could explain use inheritance, Geison rightly argued that too much has been made of this (Geison 1969). The concept was designed to explain a variety of issues, most prominently reversion. From the perspective of its reception, Holterhoff similarly noted that contemporaries believed the theory to be aligned to Darwin's earlier writings and did not necessarily emphasize its relation to use inheritance (Holterhoff 2014).

[16] To Charles Kingsley. 10 June [1867]. Darwin Correspondence Project, "Letter no. 5567," accessed on 14 February 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-5567.xml; emphasis mine.

Similarly, in the fifth edition of *Origin* (1869), Darwin recognized Jenkin's argument that single variations would get swamped through interbreeding whereas individual differences would not. Nevertheless, he suggested the importance of a form of variation "which no one would rank as mere individual differences" (1869, p. 105). Even if an individual variation itself would be swamped, the inherited constitution could (re-)produce the variation under similar conditions. Consequently, if similar conditions were to affect even only a small percentage of the population, it would produce the same beneficial variation for everyone in the group. Survival of the fittest would determine whether this new group would then replace the original group. From its initially smaller locality, the new variety of beneficially modified individuals could slowly spread in an "ever-increasing circle" (1869, p. 106).

Consequently, Darwin maintained his double conceptualization of variation. He could simultaneously think of individual differences as both the *diffusion* of a quality and the *displacement* of a population's quantitative mean until Jenkin's critique forced him to divorce the two. This divorce forms the basis of the struggles between Wallace's selectionism and de Vries's mutationism.

Alfred Russel Wallace versus Hugo de Vries: Creative Quantities and Contingent Qualities

Both neo-Darwinians and mutationists believed they were the true heirs to Darwin, each replacing Darwin's "philosophic indecision" on the relationship between selection and variation with a concrete theory. Many neo-Darwinians asserted that de Vries's argument regarded merely the size of variations. For example, Poulton argued that "the Mutationist holds … that environment selects the fittest from among a crowd of *finished products*. The Darwinian believes that the *finished product* or *species* is gradually built up … the small and not the large become the steps by which evolution proceeds" (Poulton 1909, p. xiii; emphasis mine). Consequently, de Vries's claim that mutationism was Darwinian could be dispatched with by documenting Darwin's critique of large, single variations (Poulton 1909, pp. xii-xiii, 254–256).

Yet this was not the only way the debate was framed. De Vries acknowledged that Wallace's theory of selection and the theory of mutation were both specializations of Darwinian theory, but they disagreed on what *kind* of slight variations Darwin was talking about (de Vries [1901] 1909, pp. 24, 199). Similarly, Hubrecht suggested that the debate was really about whether "fluctuating" individual differences or "chance" variations produced the material of selection (Hubrecht 1908, p. 630). Younger biologists—directed by Darwin's 1869 letter to Wallace and changes to the fifth and sixth edition of the *Origin*—could not appreciate how the readers of Darwin's earlier work led biologists "on his example, to leave a due share to single variations" (Hubrecht 1908, p. 631). Even before Jenkin, differences on this issue had been apparent between Wallace and Darwin.

In 1866, Wallace had complained to Darwin about statements in the *Origin* that suggested that "favourable variations are rare accidents, or may even for long periods never occur at all."[17] Instead, he argued, Darwin should consistently emphasize the abundance of individual differences so that if a population was large enough, "the required variety is always found, and can be increased to almost any desired extent" (Wallace 1870a, p. 289). In his later *Darwinism* (1889), Wallace continued to argue that Darwin "did not fully recognise the enormous amount of variability that actually exists" (Wallace 1889, p. 82). The book is filled with examples of continuous variation within animal populations, further illustrated with normal distribution curves that showed that quantitative differences in all directions could be found. Consequently, selection was always possible, as *every* generation would have a considerable number of individuals vary "in the two directions of excess and defect in relation to the mean amount" (Wallace 1889, p. 144).

Color differences did not fit neatly into this quantitative approach, but Wallace had already suggested that color variations could be abundantly present as these were unrelated to structure (Wallace 1870b, p. 50). More consistently, Weismann argued that what appeared as "qualitative" variations, such as the appearance of a new color, were in actuality "quantitative." The appearance of the color red, where it did not exist previously, was really just an increase in certain molecular constituents already present and a decrease in other molecular constituents (Weismann 1904, p. 151). What Jenkin had identified as limits in variation, Wallace argued, were limits imposed by selection. The conditions of life limited speed increases in racehorses, while increases in the number of tail feathers in fan-tailed pigeons were curtailed by the negative impact on their health (Wallace 1870a, pp. 292–294).[18] Selection was truly the only *creative* actor.

For Wallace, chance existed for the individual, who had their variation thrown upon them, rather than the population, which always carried the most favorable variation necessary for selection.[19] Some Darwinians followed Wallace in this respect. Gayon has noted how Karl Pearson assumed randomness in his biometrical statistics, thereby putting no limits on the power of natural selection to direct a population mean indefinitely (Gayon 1998, p. 254). Stoltzfus and Cable have suggested that early geneticists rightly criticized neo-Darwinians like Ronald Fisher for assuming that mutations were random and undirected and neglected possibilities of variation bias (Stoltzfus and Cable 2014, pp. 527–529). Beatty has noted how many architects of the Modern Synthesis used the abundance of gene recombination to suggest selection could direct populations indefinitely (Beatty 2019).

[17] From A. R. Wallace, 2 July 1866. Darwin Correspondence Project, "Letter no. 5140," accessed on 13 January 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-5140.xml

[18] Due to the supposed abundance of variation, Wallace ascribed constancy in species to the constancy of conditions. Although selection would weed out any unfit to the current conditions, it would not initate divergence until there was a change in conditions, whether in geography, climate, or the relation with other species (Wallace 1889, pp. 103–104).

[19] Of course, species could still go extinct if the conditions changed at too fast a rate, because variations were always slight.

In his reply to Wallace's 1866 letter, Darwin agreed he had perhaps overemphasized rarity, but he felt Wallace went too far in the opposite direction.[20] If beings always varied in every part, he suggested, why would there be such diverse solutions to the same problems? We have already noted Darwin's differentiation between the variation potential of *generic* and *specific* traits. Even in the fifth and sixth editions of *Origin*, Darwin continued to acknowledge the rarity of variations. In the fifth edition, he still used a phrase from the first edition about how useful variations "should sometimes occur in the course of thousands of generations" (Darwin 1869, p. 92).[21] Regarding the apparent constancy of species for long periods of time, he maintained that the speed at which selection accumulated variations was contingent on several factors—starting with "the variations being of a beneficial nature" (Darwin 1859, p. 314; 1872a, p. 291). Darwin's emphasis on relative rarity thus introduced contingency into the evolutionary process by "chance" variation.

In a discussion of Darwin's *Fertilisation of Orchids* (1862), Beatty argues that it illustrated how Darwin believed morphological differences were created through selection of "whatever differences *chance* to arrive" (Beatty 2006, p. 633; emphasis mine). If a problem had multiple solutions, the direction of natural selection would be determined by whichever favorable direction had the initial variation show up first. For instance, Darwin thought the orchid labellum had stood upwards in the ancestral orchid but were usually downwards in living species, which had been achieved by a twisting of the stalk or ovarium. Some species had gone back to an upwards labellum, but where *Catasetum* untwisted itself to achieve this, *Malaxis Paludosa* had done so by twisting itself even further (Beatty 2006, pp. 633–634).

De Vries pointed to Darwin's many references to the rarity of chance variations as the basis of his mutation theory. As in Poulton's characterization, de Vries has often been accused of supporting a belief in "large-scale" mutations that gave rise to new species (for example: Huxley 1942; Smocovitis 1992; Gould 2002). Garland Allen went as far as to suggest that de Vries believed mutant forms to be "infertile with their parents," which de Vries could only overcome by emphasizing similar mutations occurring in multiple individuals at once (Allen 1969, pp. 60, 72).[22] There is little evidence that this is what de Vries suggested.[23] De Vries argued that his mutations were similar to Darwin's "single variations" and were noticeable for being "*sudden* though *minute*" (de Vries [1901] 1909, p. 4).[24]

[20] To A.R. Wallace. 5 July [1866]. Darwin Correspondence Project, "Letter no. 5145," accessed on 13 January 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-5145.xml

[21] He removed "sometimes" in the sixth edition (Darwin 1872a, p. 63).

[22] Allen does not cite de Vries for evidence but refers to three other writers. One of these does argue for the theoretical necessity of variations appearing multiple times to counteract reproductive isolation, but before de Vries's theory was even published. The two others are more contemporary, but they do not focus on the reproductive isolation at any point.

[23] More nuanced is Bert Theunissen, who emphasized that de Vries called crossing between genetically identical individuals "normal" fertilization, whilst other forms of crossing were relatively rarer (Theunissen 1994, p. 244). This is certainly correct, but we should distinguish this from Allen's claim, which suggests reproductive isolation.

[24] In Darwin's work, *sudden* often appears to be synonymous with *large*. So this indicates a different interpretation on de Vries's part. The original reads: "Eine, wenn auch *geringe*, doch *plötzlinge* Umänderung" (One, albeit small, but sudden change) (de Vries 1901, p. 4).

Of course, some of de Vries's own studies on Lamarck's evening primrose showed considerable size changes. Yet, for de Vries, the *perceptibility* of change was more important than its *size*; if even long term changes were imperceptible, there would be no material for experimental investigation (de Vries 1901, p. viii).[25] Hence, he rejected the term *sport*, which unnecessarily suggested large size (de Vries [1901] 1909, p. 39). As Hubrecht noted: "unobserved by the untrained eye, [mutations] can as yet only be detected by the specialist" (Hubrecht 1904, p. 218).[26] In response to W. B. Scott's critique that paleontological series in the horse showed continuous progression "*by almost imperceptible gradations*," de Vries argued that these (only just perceptible) gradations would be considered steps. Observing continuity or discontinuity here depended largely on one's point of view (de Vries [1901] 1909, p. 48). Similarly, Thomas Hunt Morgan noted that de Vries's emphasis on constancy rather than size made it compatible with Darwin's disregard for large sports (Morgan 1903, p. 297; see also 1918, p. 365).[27]

De Vries's insistence on mutations creating new species and varieties appears to run counter to this, but as Kingsland reminds us, de Vries often gave terms unique, circular definitions (Kingsland 1991). He distinguished between taxonomic, *collective* species (also called Linnean species), on the one hand, and genetic, *elementary* species on the other (de Vries [1901] 1909, p. 171). Collective species were aggregations of elementary species that could be genealogically linked back to one another and had no extinct forms separating them. The historical study of the gaps between elementary species would reveal the origin of collective species. In contrast, elementary species revealed the origin of specific characters through physiological investigation (de Vries [1901] 1909, p. 56). Each specific element, or set of characters, was represented in the germ by a unit named a *pangen* (sometimes translated as *pangene)* (de Vries [1901] 1909, p. 171).

Building on Darwin's hypothesis, de Vries named his theory of heredity *Intracellular Pangenesis* (1889). He divided the theory up into two fundamental propositions. He agreed with Darwin that each individual hereditary character, if able to vary independently, possessed its own material unit within the germ.[28] He preferred

[25] De Vries noted that the Darwinian theory posed "infinitesimal, ordinarily invisible variations" while mutation posed "small but distinct steps, each step corresponding to one or more unit-characters" (de Vries 1919, p. 213).

[26] Similarly, Shull noted that "the eye of the breeder learns to seek for mutational variations, and this search must result in the discovery of many instances of mutation of lesser magnitude … than was formerly required to force themselves upon his attention" (Shull 1907, p. 63).

[27] Allen argued that Morgan started having doubts about the role of sizeable, discontinuous mutations, as de Vries understood them, when his study of *Drosophilia* convinced him of this (Allen 1968). However, Morgan argued from the very beginning that de Vriesian mutations could be very small. He insisted that "numerous mutations are smaller than the extremes of fluctuating variation" (Morgan 1903, p. 289; see also Morgan 1918, p. 365). Allen cites Morgan's claim that "there are variations within the limits of Linnaean species" as a criticism of de Vries, but, as we shall see, de Vries believed in very much the same thing (Allen 1968, p. 129).

[28] Darden noted that de Vries reframed pangens to represent hereditary characters for independent characters, while Darwin thought gemmules carried hereditary characters for their cell only (Darden 1976, p. 148).

to call these units pangens rather than gemmules. Second, he criticized Darwin's "transportation hypothesis"—the claim that cells threw off pangens at each stage of development to be transported to the germ cells (de Vries 1889, p. 64). Rather, drawing on cell theory, he argued that the pangens were kept intracellularly within the cell nucleus and spread through cell division.

Darwin's hypothesis, de Vries insisted, differentiated between two kinds of heritable variability (see also Darden 1976). First, nutrition influenced the relative quantities of a pangen, which led to quantitative"fluctuations" of the existing characters. These formed the continuous individual differences within elementary species, as used by Wallace, where inheritance was limited within Jenkin's sphere. Second, he agreed the quality of pangens themselves could change, though not due to the inheritance of acquired characters. Rather, *progressive* mutations formed new pangens, while degressive and retrogressive mutations caused existing pangens to activate or deactivate respectively. New pangens determined the development of new characters, thereby increasing differentiation between species (de Vries 1889, p. 74). As the real elements of evolutionary change, pangens determined the pedigree of elementary species. Consequently, "the number of identical pangens in two species is the true measure of their relationship," and "systematic difference is due to the possession of unlike pangens" (de Vries 1889, p. 73).

By definition, progressive mutation created new elementary species because the appearance of a new hereditary element signaled a discrete, genetic unlikeness. So when German Darwinian Ludwig Plate (1862–1937) suggested that evolution was discontinuous in the hereditary particles and continuous in the external expression, de Vries argued this "conceded the main point in discussion" (de Vries 1914, p. 527). In single traits, quantitative fluctuations of a mutation were large enough for ranges to overlap with those of other qualitative mutations—this was *transgressive variability*. Two approaches could resolve this. First, each pangen influenced the state of surrounding pangens, so mutations caused slight differences in multiple characters at once. By studying these correlations, the common qualitative element could be inferred (de Vries [1903] 1910, pp. 426–468, 1904, p. 12). Second, quantitative studies could emphasize the average value of many offspring rather than an individual's visible characters (de Vries 1904, pp. 813–814).[29]

Consequently, de Vries disputed that Wallace (and Weismann) were correct to only characterize populations by quantitative differences. Charles Benedict Davenport (1866–1944), director of the Station for Experimental Evolution at Cold Spring Harbor, New York, defended de Vries by arguing that Weismann was wrong to describe color variations as quantitative. The appearance of a red pigment where none previously existed could be described as moving from 0 to 1, but this would overlook the qualitative chemical change that would have needed to occur (Davenport 1909, pp. 162–163).

[29] To get a clear figure for the relative value of an individual plant, de Vries suggested growing two to three hundred offspring and ascertaining their average value (de Vries 1904). This could be compared to the value of 50 more individual plants, also to be determined by growing and measuring two or three hundred of their offspring.

For de Vries, populations were amalgamations of qualitatively different elementary species or varieties, and crossing between these could produce new elementary types by recombining the available specific elements (and hence characters) (de Vries [1901] 1909, p. 72). In the wild, even isolated mutants could reproduce their newly acquired trait by crossing with related elementary species and would spread the mutation if advantageous (de Vries 1903, pp. 503–509). In the long run, a single new unit could double the available elementary types through natural crossing, while ten independent mutations could eventually multiply the number of types within a population thousand fold (de Vries 1907a, pp. 82–84; 1907b, p. 212). Crediting experimental evidence from Swedish experimenter Hjalmar Nilsson (1856–1925), he argued that many varieties had sufficient elementary forms to be selected for any commercially relevant trait, which "not rarely" included new mutations in the direction which was previously selected (de Vries 1907a, pp. 89–90). Such "mutability" would be periodic, with species oscillating between periods of plentiful mutation and stability. This explained why barley had shown few novelties, and thus had provided little opportunity for change.

In other words, selection was *contingent* on the available variation, which followed its own logic. The same variation often recurred multiple times in individuals of the same species or even in widely different species. This recurrence suggested that an internal cause akin to Darwin's analogous variation was at play, which would increase the chances of single variations finding favorable conditions for themselves (de Vries 1904, pp. 242–244, 701–703). At other times certain variations were absent. With regard to color, how one could select for a "blue Dahlia" or "bright yellow Hyacinth" (de Vries [1901] 1909, p. 58)? If desirable, the careful selection and (artificial or natural) self-fertilization of individual plants could provide such purity that the resulting strain was independent of selection—until new crossings or mutations took place (de Vries 1904, p. 150; for the similar views of Wilhelm Johannsen, see Roll-Hansen 1989).[30]

Despite this contingency, de Vries argued that natural selection was the one directing cause of the broad lines of evolution (de Vries 1904, p. 7). Differences between elementary species were relatively small, so definite variation alone could not explain "the beautiful adaptive organizations of orchids, of insectivorous plants and of so many others" (de Vries 1904, p. 572). Harmful and neutral mutations persisted for a shorter or longer time, while selection would accumulate into structures those mutations that prevented offspring being crowded out (de Vries 1904, pp. 572, 597). Selection chose not between Poulton's *finished* products but would *finish* products based on available steps. De Vries acknowledged the *directive* power of natural selection and limited only its *creative* power by allowing for the chance nature of variations.

[30] De Vries believed this lack of crossing was crucial for productivity in commercial farming, but was to some extent unnatural. *Vicinism* was the term he used to denote the prevalence of such crossing. It was "not at all easy to keep the common varieties of cereals pure … even the best are subject to the encroachment of impurities … the purity of the races is a condition implanted in them by man, and nature always strives against this arbitrary and one-sided improvement" (de Vries 1904, pp. 101–102).

Wallace and de Vries's struggle was not one of Darwinism and anti-Darwinism, but between two Darwinian conceptions of the role of chance in variation. Darwin's variation could be interpreted as quantitative and abundant, or qualitative and relatively limited. To Wallace, chance uncertainty existed at the level of the individual but not the population. To de Vries, every level was characterized by contingency due to single variations. It will come as no surprise that many experimenters supported de Vries's theory, and that de Vries was asked to dedicate the Station for Experimental Evolution at Cold Spring Harbor in 1904 (Allen 1969; Kingsland 1991). Both the director Davenport and plant geneticist Shull explicitly defended de Vries's selection of elementary qualities as Darwinian (Davenport 1909; Shull 1905). Interestingly, de Vries found support not just from fellow experimenters but also morphologists. Hubrecht's support for chance variations has already been noted. Among the neo-Darwinians, however, even Lankester suggested that Darwin thought that variation was limited by the physical and chemical constitution of the individual.[31]

The role of chance variations within morphology is discussed in the following section. By relating Thomas Henry Huxley's work to Darwin's conception, I hope to show that there was much continuity in this debate—from the eclipse period back to the non-Darwinian revolution.

Typology for Darwin and Thomas Henry Huxley: Selective Classification and Constraints

Bowler argued that the non-Darwinian revolution did not lead to an acceptance of natural selection as the mechanism of evolution. Rather, it instigated acceptance of evolution as a theory and led morphologists to historical, phylogenetic reconstructions of the animal kingdom. These "non- " or "pseudo-Darwinians" supposedly did not appreciate Darwin's open-ended branching pattern of evolution and saw the "history of life as the unfolding of a preordained pattern toward a predictable goal" (Bowler 2009, p. 436). In addition, the morphologists engaged in their reconstructions "against Darwin's advice" (Bowler 1988, p. 75). Mayr argued that morphologists commonly ignored adaptation as a crucial component of the Darwinian program in favor of structure and type (Mayr 1982, p. 467). The emphasis on *type* was problematic, due to its connection with essentialism, or the characterization of groups as "fixed and unchanging forms" (Mayr 1982, p. 38). Darwin had supposedly contributed to ending essentialism, because his *population thinking* stressed individuality and acknowledged that types were only abstractions (Mayr 1982, pp.

[31] Lankester illustrated this by suggesting that no amount of selection could ever turn a beetle into a mammalian vertebrate because of paramount constitutional differences. This was forgotten by those hoping to find "opportunity" for natural selection by claiming slight variations "in every direction around a central point" (Lankester 1907, p. 9).

45–46). Still, he accused Darwin of occasionally "falling back" into this himself (Mayr 1991, p. 108).[32]

However, the interest in phylogenetic reconstruction can hardly be described as merely a generic evolutionary or specifically non-Darwinian endeavor**.** It has already been noted that Darwin thought variation was linked to common descent, but he also thought it played an important role in the classification of the animal world. Although the discussion of classification and morphology was a relatively small section near the end of the *Origin*, we should acknowledge that both topics connected to the previous chapters in essential ways. For instance, Darwin noted that a new systematics had to be formulated based on descent in the form of a pedigree. Species should be classified as groups of individuals sharing a common ancestor, which in turn were subordinated to groups of species sharing an ancestor even more remote, and so on, to give rise to further taxa, i.e., genera, sub-families, families, sections, orders, and classes (Darwin 1859, pp. 413, 422). "Dominant" species (which have large populations and are widely distributed) would be most likely to have favourable variations. Hence, natural selection suggested that dominant species would produce new dominant species—the largest groups tend to increase further in size and diversity at the expense of smaller groups (Darwin 1859, p. 433). This process "explains the arrangement of all forms of life, in groups subordinate to groups, all within a few great classes" (Darwin 1859, p. 471; see also p. 428). Gaps between species could similarly be explained by species outcompeting their parent forms, and thus leaving no transitional links alive (Darwin 1859, pp. 172–173).

As adaptive characters were signs of divergence, Darwin acknowledged that classification should focus on the non-adaptive. Already in the first edition of *Origin* (1859), Darwin emphasized that it was important to study the *unity of type* revealed by morphology to uncover lineages through non-adaptive traits (p. 434). In the fifth edition (1869), Darwin suggested that morphologically important characters were likely due to "definite action of the conditions of life, causing all or nearly all the individuals of the same species to vary in the same manner" (Darwin 1869, p. 151). Traits like mammalian hair, avian feathers, and reptile scales, he concluded, had remained constant due to their lack of physiological importance. This constancy made them highly important for classification (Darwin 1869, p. 157). Similarly, Gregory Radick later reminded us that Darwin's non-adaptive account in *The Expression of the Emotions in Animals and Man* (1872b) was necessary for him to prove the relatedness of human and non-human animals, as well as the close relation between different human races (Radick 2010). Nevertheless, Darwin maintained that it remained possible that many morphological traits had been adaptive for precursors or were correlated with adaptation.

[32] The assumption of the interconnectedness between typology and essentialism has been challenged. Polly Winsor has noted the shaky foundations on which Mayr's thesis rested (Winsor 2006). Levit and Meister similarly asserted that typology could supplement Darwin's evolutionism because pure typology considers types to be abstractions only (Levit and Meister 2006, p. 300). It depends on the individual researcher, and their additional theoretical assumptions, whether they are essentialist or opposed to population thinking.

After publishing the first edition of the *Origin*, Darwin increasingly emphasized the importance of typology. Even where natural selection could direct modification, each organism possessed "different materials or variations to work on, in order to arrive at the same functional result; and the structures thus acquired would almost necessarily have differed" (Darwin 1872a, b, p. 153). We have already noted Beatty's observation that Darwin's *Fertilisation of Orchids* (1862) emphasized chance variation; in Darwin's understanding, even among closely related organisms, the same structures could be modified along very different lines to meet the same end goal. The possibilities for different lineages were determined by the common progenitor's existing form, and earlier variations of type determined which future variations could be considered favorable (Beatty and Desjardins 2009, p. 242). Unfortunately, Beatty does not dwell on Darwin's use of this typological method; it appears to me to be crucial. In *Orchids*, Darwin argues particularly forcefully for the importance of ideal types and homology as tools of evolutionary science. For example:

> No group of organic beings can be well understood until their homologies are made out; that is, until the general pattern, or, as it is often called, the ideal type, of the several members of the group is intelligible. … [T]he science of homology clears away the mist from such terms as the scheme of nature, ideal types, archetypical patterns or ideas, &c.; *for these terms come to express real facts*.… [W]hether [the naturalist] follows embryological development, or searches for the merest rudiments, or traces gradations between the most different beings, he is pursuing the same object by different routes, and is tending towards the knowledge of the actual progenitor of the group. (Darwin 1862, pp. 287-288; emphasis mine)

Darwin's interest in the *ideal type* to find *the actual progenitor* served two distinct purposes. First, it allowed for classification in drawing attention to the unity of type among groups of animals due to a common ancestor, as this unity was exhibited by organisms "independently of their habits of life" (Darwin 1859, p. 434). Second, in establishing the ideal type, it could be revealed how this type was refashioned in different manners to serve similar goals. Amundson has criticized claims that morphologists were only interested in charting the *historical* path of evolution, not its *causal* mechanism (Amundson 2005, pp. 233–243). He suggests that the morphological emphasis on form brings discussions of causal developmental opportunity and constraint to the fore, and that this was a crucial proof of Darwin's belief in common descent (Amundson 2005, pp. 129–134). Darwin was not a morphologist, but he appreciated the need for typology to understand why certain evolutionary pathways were taken over others.

Let us take the example of Thomas Henry Huxley as a foremost exponent of phylogenetic reconstruction. Although Huxley himself had supported Darwin, it has been well established that this had never precluded his awareness that natural selection was incomplete as a mechanism. In his review of *Origin*, Huxley had suggested that Darwin had given a good mechanism for structurally different (morphological) species, but not sexually incompatible (physiological) species (Huxley 1860a, b, pp. 552–556). Michael Bartholomew argued that Huxley's work never came to incorporate Darwinian theory and he remained wedded to saltationism and persistency of type (Bartholomew 1975; see also Huxley 1860a, b, p. 569; Huxley [1864] 1893b, p. 97). Michael Ruse noted how Huxley kept evolutionary theory out of his official teaching and used it in public lectures only (Ruse 2009, pp. 219–221). Mario Di Gregorio argued that Huxley should be considered less a Darwinian than an outgrowth of German morphology (Di Gregorio 1982). In a review of Haeckel's *Natürliche Schöpfungsgeschichte* (1868), Huxley himself started off by noting how "Germany now takes the lead of the world in scientific investigation" (Huxley [1869] 1893c, p. 107). In following Haeckel, however, Huxley, I would argue, increasingly used Darwinian logic.[33]

In the passages where Huxley criticizes Darwin's denial of saltationism, he lauds his explanation for the absence of transitional forms through extinction (Huxley 1896, pp. 76–77). Winsor argues that Darwin's assumption of species branching off and going extinct was a novel approach to classification because previous scholars had only used living forms (Winsor 2013, p. 74). Sherrie Lyons convincingly contends that Huxley's openness to saltationism was tied to the state of the fossil record, and he had softened when gaps were slowly being filled in by the time of his 1868 study of *Archaeopteryx* (Lyons 1995). From 1868 onwards, Huxley's speculations on evolution show a conspicuous absence of "saltations." In his study of forms intermediate between birds and reptiles, Huxley specifically asked how it could be that "if all animals have proceeded by *gradual* modification from a common stock, that these great gaps exist? We, who believe in Evolution, reply, that these gaps were once non-existent" (Huxley 1868, p. 304; emphasis mine). This emphasis on the gradual nature of evolution returns again and again.

In his 1876 lectures "on the Evidence as to the Origin of Existing Vertebrate Animals," Huxley took time to note the wonderful differences between birds and reptiles, i.e., feathers versus scales, warm-bloodedness versus cold-bloodedness. Yet, a deeper analysis revealed that "birds are modifications of the same type as that on which reptiles are formed," and under perfect conditions, one would expect to find "an exact series of links" (Huxley [1876] 1902a, p. 179). In noting the prevalence of *Pterodactyles* in the fossil record, Huxley noted that they could be considered very bird-like reptiles but should not be thought to elucidate anything in the relation between those two groups of animals.

Like birds, *Pterodactyles* had evolved to gain wings, air cavities within bones, a keel, and probably warm-bloodedness. However, the various similarities could be considered "purely adaptive" (Huxley [1876] 1902a, p. 177).[34] Both modified a reptilian type and appeared to serve the same end, but they were not necessarily constructed along the same lines. *Pterodactyle* wings were more akin to a bat's wing, and thus they were about as useful in classification as bats would be as a bridge

[33] To say that Haeckel's *Generelle Morphologie* (1866) fascinated and energized Huxley appears to me undeniable, but Huxley remained sceptical of the ease by which Haeckel produced his phylogenies. As he wrote to Darwin in January 1867, he had already constructed multiple "trees," but lacking were the criteria to judge their applicability, and he could not but "entertain a certain shyness of these speculations." See: from T. H. Huxley. [before 7 January 1867]. Darwin Correspondence Project, "Letter no. 5343," accessed on 15 February 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-5343.xml.

[34] In the same passage in his 1870 talk, Huxley referred to them as "merely adaptive."

between birds and mammals (Huxley [1876] 1902a, p. 181; see also Huxley [1868] 1901a, p. 308). Similarly, the state of the winged arms contrasted markedly with the state of the claws. Despite their grounded nature, *Dinosauria* more convincingly evidenced that the gap to birds could be bridged other than from a flying reptile. It was more convincing exactly because the similarities in traits between *Dinosauria* and birds could not be reduced to adaptations to similar habits of life.

Huxley was wary of presuming that the relatively few fossils available showed how gaps between species *had been* bridged and emphasized how gaps between types *could* be bridged. In his Anniversary address to the Geological Society in 1870, he noted the differences between intermediate forms as *intercalary* types and *linear* types (Huxley [1870] 1901b, p. 530). The term linear had to be reserved for describing a genetic lineage, which Huxley compared to the "fathers and sons" of the types involved. Intercalary types showed how a form was structurally intermediate between two other types, but did not posit a direct, genetic relationship between them. Huxley suggested that these types could be considered the "uncles and nephews." All intermediary connections between birds and reptiles, such as *Archaeopteryx* and the *Dinosauria,* appeared to be intercalary. In other words, these forms were likely to be more distant uncles and nephews, and they merely showed how the gap could potentially be bridged. *Pterodactyles* had most clearly "gone off the line," for despite their flying habits and other structural similarities to birds, their wings did not remotely resemble (Huxley 1877, p. 70). Huxley, in other words, was not drawing neat, progressive, linear pedigrees.[35]

This interpretation does not imply that progressivism was completely absent from Huxley's work. In his 1876 lectures, Huxley would note that one could see in Mammalia "the perfection of animal structure" (Huxley [1876] 1902a, p. 183). Following Haeckel, he took "the successive stages of embryological development" and "the successive stages of the evolution of the species" to be crucial to taxonomy (Huxley [1880] 1902b, pp. 460–461). In his 1880 classification of the Mammalia, he divided mammals progressively into the Prototheria, Metatheria, and Eutheria. The Prototheria was considered the most primitive group, and it contained both existing monotremes and extinct forms of a similar type. The Metatheria had progressed from these and consisted both of existing marsupials and extinct forms of a similar type. Progressive development culminated in the Eutheria, which was made up of living and extinct placental mammals.

Nevertheless, Huxley argued that the more specialized living monotremes would not resemble the more basic Prototheria from which the basic Metatheria and basic Eutheria had evolved. Similarly, the marsupials alive today were likely to be a highly specialized branch of the Metatheria, with many of their traits highly divergent. Huxley argued that the structure of current marsupial feet suggested that they were probably all derived from an arboreal form. For this predecessor, it would be "advantageous" to give birth as soon as possible and feed offspring through lactation rather than through "an imperfect form of placenta"

35 The study of horses gave Huxley more hope at a linear arrangement, but even here he remained sceptical that a true genetic relationship was established (Huxley 1877, p. 84).

(Huxley [1880] 1902b, p. 466). Extinct Metatheria would probably have lacked specialized pouches and early births and shown transitional morphological traits between living marsupials and Eutheria. Consequently, Huxley was specifically invoking ancestral adaptation to certain habits of life as an explanation of the shared traits of living marsupials. I would argue this was possible because these living marsupials did not share habits of life, yet showed a common deviation from extinct Metatheria. That marsupials all shared their divergence was likely due to an adaptation to a common marsupial ancestor's habits of life.

In Huxley's discussions of the persistence of type, he similarly looked to adaptation as the solution to the problem. The great French zoologist Georges Cuvier (1769–1832) had attempted to show the persistence of type by comparing non-human animal mummies from Egypt to their contemporary counterparts. He found no significant change. Huxley argued that if the process of evolution was connected to surrounding conditions, the stability of Egyptian conditions could easily explain this stability in form (1877, pp. 33–34). Persistence of type was only lethal to theories that posited some internal mechanism that would necessarily modify. As Darwin had argued, life conditions determined whether variations were likely to replace their parent form based on their relative fitness. Modification of form was contingent on the *chance* appearance of favorable variations and not a necessity (Huxley 1877, p. 40).

In his attack on Darwin, Mivart had asserted that Darwinians believed variations would be "in *all directions*" and "*infinitesimal*," yet it was more probable that they would appear in a definite direction (Mivart 1871, p. 34). In his response to Mivart, Huxley criticized him for characterizing Darwinian variation as being "fortuitous" and taking place "in all directions" (Huxley [1871] 1893a, p. 181). Constant variation was a crucial element of Darwinian theory, but "it is limited by the general characters of the type to which the organism exhibiting the variation belongs" ([1871] 1893a, p. 181). By way of example, Huxley noted that a whale will not tend to vary in the direction of feathers or a bird toward whalebone. Darwin's theory, he affirmed, was one of variation "aided by the subordinate action of natural selection" ([1871] 1893a, p. 181). In his American lectures, Huxley spoke of Darwin's great contribution as having "shown that there are two chief factors in the process of evolution," namely, that organisms tend to vary and the relation of those variations to the external conditions of life (1877, p. 39). In "Evolution in Biology" (1878), Huxley again affirmed that variation would proceed in a limited number of directions by virtue of certain inherent conditions of the organism ([1878] 1893d, p. 223).

The subordination of natural selection and emphasis on variation may appear anti-Darwinian. It expresses, however, three main elements from Darwin's work that Huxley understood very well, namely, the contingency of directive selection on the availability of variation, the survival of initially non-advantageous variations in species, and the developmental limitations on variation. On the first, he argued that selection never pretended to initiate change, because Darwin himself had noted that selection cannot direct until favourable variations appear (Huxley [1888] 1893e, pp. 288–290). On the second, Huxley acknowledged that the theory posited that species come about through the selection of advantage, but Darwin had admitted that various traits could persist by being indifferent in that regard. On the third, the existing constitution determined the nature of variations.

Although Huxley was unwilling to commit himself fully to an unproven theory, he continually stressed how the facts could be brought in alignment with natural selection in contrast to alternatives. Huxley's research program largely excluded adaptation, but such was the way that Darwin had set up the importance of classification. Non-adaptive characters were more reliable to prove common descent than adaptive characters, so these had to be clearly delineated. Huxley's preoccupation was not merely with evolutionism but with a Darwinian version that he hoped would come to explain ever more facts. The *structural* Darwinian concern of common descent, typology, and law-abiding variation undoubtedly created tension with the study of *creative* natural selection. In this, the so-called pseudo-Darwinians followed Darwin's concerns as exhibited by *Fertilisation of Orchids* (1862), *Variation under Domestication* (1868a, 1868b), and *Expression of the Emotions* (1872b).

Geographical Problems of the Eclipse

The existence of several streams in Darwinism complicates the slightly different eclipse narratives promoted by both *The Non-Darwinian Revolution* (1988) and *The Eclipse of Darwinism* (1983). It leads to an interesting geographical note as well.[36] Like Julian Huxley, Bowler associated Darwinism explicitly with a few key figures (usually British), such as Karl Pearson, Raphael Weldon, Alfred Russel Wallace, Edwin Ray Lankester, and Edward Poulton. August Weismann serves as a German exception that confirms the rule. Outside this group, different conceptualizations of selection and variation persisted.

Curiously, this notable concentration of Darwinism in Britain in particular is only occasionally commented on by Bowler. Opponents are recognized as coming from places as varied as the United States, France, Germany, Austria, and the British Empire. Although anti-Darwinism is largely discussed in general terms, Bowler does give us two more geographically oriented chapters. The French and American schools of thought are outlined because ignorance of, or antagonism to, Darwinism had been institutionalized within these countries from a relatively early stage. Internalist histories of science, Jonathan Harwood reminds us, draw on comparative studies only when they believe "normal development was stunted in a particular country due to unusual conditions," and he identifies French disinterest in Darwinism as an

[36] For an overview of geographical approaches, see Livingstone (2003) and Finnegan (2008).

example (Harwoon 1993, p. 4).[37] Not only do I agree, but I would also argue this assessment extends to the American school as well.[38]

Indeed, apart from these exceptions, most of the debates in the book remain placeless. They do not emphasize the role of local traditions on individual actors' support or opposition to Darwinism. When geography occasionally does shine through, however, it weakens the eclipse narrative. If British support for Darwinism continued from an earlier stage, and French and American doubts about Darwinism continued from an earlier stage, one is forced to wonder *where* exactly this eclipse was taking place. If many places saw only a limited popularization of natural selection, then the absence of support during a later period could not have been an eclipse. It also, far more interestingly, suggests the opposite. If *selectionist* Darwinism had never been that popular in a place, is it not significant to see people engage with that theory in this locality at a later time?

Two main sources for the eclipse narrative focus largely on the German situation: botanist Eberhard Dennert's *At the Deathbed of Darwinism* (1904) and Erik Nordenskiöld's *The History of Biology* (1928). Dennert's provocative title is taken to signify the confidence of Darwin's adversaries, which in turn is alleged to indicate their strengthening position (Bowler 1983, p. 4). It is interesting to note here that in direct response, American entomologist Vernon Kellogg titled the introduction to his *Darwinism To-Day* (1907) as "Introductory: the 'Death-Bed of Darwinism.'" Kellogg noted that such declarations had been as old as Darwinism itself, "proving prejudice or lack of judgement or of knowledge" (Kellogg 1907, p. 1). Dennert's introduction to a collection of papers by German scientists made it very clear that the book's main purpose was to illustrate the death of a supposed "scientific disproof of the very foundations of the Christian faith" (Dennert 1904, p. 27). Associating Darwinism with both materialism and monism, he argued that new research was paving the way for the recognition of a "definite plan" underlying nature, as well as the need for the independent creation of the human soul (1904, pp. 33–34).

The reference to monism is useful here because it is less connected to Darwin than to his German popularizer, the morphologist Ernst Haeckel. Haeckel's advocacy of monism (oneness) explicitly served to counter Christian dualism, and this struggle with religion has been well documented (see Lustig 2002; Richards 2005, 2008, 2013, pp. 240–241). Dennert believed his generation built on the work of

[37] Camille Limoges argues that the French closely followed British debates regarding the meaning of Darwinism. In response to the attempts to expunge all Lamarckism from evolutionary theory, together with political motives in the French Third Republic to promote Lamarck as a heroic national figure, a regrouping took place in France around neo-Lamarckism (Limoges 1976, p. 183). Lauren Loison notes, however, that this group was highly diverse and unified only in their interest in "plasticity" and "heredity" (Loison 2011). Burian, Gayon and Zallen have convincingly discussed how "Lamarckian" French biologists held aloof from genetics (and hence the Evolutionary Synthesis), yet their alternative traditions were later able to contribute to cutting edge genetic research that led to the rise to molecular genetics (Burian et al. 1988). French biologists studied heredity through the lens of the physiology of Claude Bernard or the microbiology of Pasteur, which provided useful non-Mendelian insights. France may thus have been most un-Darwinian, but non-selectionist views are not necessarily problematic.

[38] An updated, and generally more balanced, assessment of the American situation is given in Largent (2013).

earlier anti-Darwinians, like the botanist August Wigand, and had overcome an era when Haeckel had made it seem "impossible for a young naturalist to be anything but a Darwinian" (1904, pp. 35–37). In his study of Darwinism in Germany, Alfred Kelly noted how anti-Darwinian Christians, like Wigand and Dennert, often mixed religious and scientific critiques. In doing so, they took their opponents' (like Haeckel) claims—for instance, that Darwinism signified atheism and materialism—for granted and ignored that the Darwinian social group contained "an extremely varied lot" who did not always represent Darwin's views (Kelly 1981, p. 98). Dennert continuously emphasized how the failure of selection is a success for theism. The American translator of the work, the young Roman Catholic priest (and later Archbishop) Edwin Vincent O'Hara, engaged with Darwin's work more directly, but uncritically cited de Vries's work as an attack on Darwinism. Furthermore, much of his preface is spent associating Darwinism with Haeckel's views, and he cited many a critique of Haeckel's Law of Biogenesis as evidence of Darwin's failure (Dennert 1904, pp. 9–25).[39]

Less religiously oriented critiques show a similar conflation. A broad overview of biology from the beginning of history to the early twentieth century, Erik Nordenskiöld's book was both deeper and further reaching than Dennert's. With the Czech biologist and philosopher Emanuel Rádl, Nordenskiöld deemed Darwin's theory an extension of English Liberalism into the biological sphere, to which he also attributed its main success (Nordenskiöld 1928, pp. 458–459, 477–478; Rádl 1930, pp. 15–19).[40] Darwin's biggest flaw was his tendency to support all-encompassing theories rather than accept that theories should address specific issues and not move beyond "the bounds of absolute necessity" (Nordenskiöld 1928, p. 473).

Nordenskiöld reiterated on several occasions that German Darwinism was different or peculiar in form. German methods followed Ernst Haeckel in prioritizing comparative morphology and embryology in a way Darwin himself had not done and weaved it into a romantic philosophical world view (Nordenskiöld 1928, pp. 492–511). Similarly, Rádl suggested that Darwinism found "its spiritual home" in Germany, and it was shaped into a "dogmatic and logical form" there (Rádl 1930, p. 42). Initial reception had been friendly, he continued, but when Haeckel mixed it with Rudolf Virchow's materialism, it took on a dangerous form of "if not a new religion, at least a new faith" (Rádl 1930, p. 52).

Darwin's scientific influence on continental biology was considered marginal, while Haeckel's investigations into embryology and morphology were more typical (Rádl 1930, p. 129).[41] Rádl argued that Haeckelian methods were so influential that it could be said "the English established Darwinism, the Germans built it up; the Germans should also tear it down again" (1909, p. 545; translation mine). Despite

[39] Haeckel's biogenetic law is perhaps better known under the simplification that "ontogeny recapitulates phylogeny," i.e., the stages of individual development follow the stages of the evolutionary line.

[40] Rádl's book was initially published in German in 1909 and Nordenskiöld's in Swedish in 1920. In a few instances, I use Rádl's original version (as will be clear from the 1909 reference), as it contains phrases not found in the translation.

[41] In Germany, Levit and Hossfeld remind us, both Darwinians and their detractors were often interested in structuralist or "typological," rather than adaptationist or "population" approaches (2017, p. 179).

acknowledging the "peculiar stamp, extremely characteristic of the age" of Haeckel's morphology and radical atheism, it was increasingly discussed interchangeably with Darwin's theory by Nordenskiöld (1928, p. 504).

Blows dealt to Haeckelian morphology by the more experimental sciences were thus also blows at Darwinism generally. The increasing importance of heredity studies, Nordenskiöld argued, had replaced Darwinism in the way "it has taken hold of the public mind and has nowadays to serve as an explanation for anything that presents any difficulty" (Nordenskiöld 1928, p. 594). Yet, in his German example of those engaged in such heredity studies, he names only two Mendelians, Carl Correns (1864–1933) and Erwin Baur (1875–1933)—before explicitly pointing out that Baur's goal is to hybridize Mendelism with Darwin's natural selection (Nordenskiöld 1928, pp. 594, 615). Similarly, he credits de Vries with kickstarting heredity studies but also notes his agreement with Darwinism "in all essentials" (Nordenskiöld 1928, p. 588).

Throughout the book, the suggestion is that Haeckel's Darwinism (as morphology and atheism) is distinct from Darwin's Darwinism, yet they are somehow also vulnerable to each other's flaws. Baur's example shows how problematic this is. His choice for working in genetics rather than morphology should be a step away from Darwinism, so how should we frame his attempt to reintegrate Darwin's theory of selection into genetics?

In his dichotomy between Darwinism and pseudo-Darwinism, Bowler follows a similar logic to Nordenskiöld (Bowler 1988, pp. 76–83). Initially, pseudo-Darwinism is considered a non-Darwinian movement based on a non-selectionist, Haeckelian morphology that became popular in Germany, (and, through Huxley and Lankester, in the United Kingdom as well). Later on, however, attacks on this pseudo-Darwinism are taken to reliably indicate that selectionism was superseded during the eclipse (Bowler 1988, p. 103). Here, the tensions between the narratives of *The Non-Darwinian Revolution* and *The Eclipse of Darwinism* are most clearly revealed.

This point is important, because if the connections between such Darwinisms are geographically bound, we might find other places where these connections do not hold. The success of the neo-Lamarckian school of thought in the United States in the latter half of the nineteenth century has been well studied (see, for instance, Pfeifer 1965; Ceccarelli 2019). Regarding the early twentieth century, both Garland Allen and Sharon Kingsland note the embrace of de Vries's theory among experimental students of heredity (Allen 1969; Kingsland 1991). It fits the broader historiographical view of experimental traditions, like Mendelian heredity, gaining a foothold at the expense of naturalist traditions, like morphology (Allen 1979).[42] Jim Endersby similarly points to its use by experimenters but also notes de Vries's claim to support Darwinism (Endersby 2013).[43] Where does that leave Darwinism?

[42] Allen changed his position slightly in light of the multiple meanings applied to the term *morphology*. Instead, he argued there was a struggle between experimental and naturalist traditions, even within certain morphological traditions (Allen 1981).

[43] These were explicitly ignored by the press, who thought stories of Darwin's demise would sell better.

In his revisionist piece on the eclipse, Mark Largent challenges the view that entomologist Vernon Kellogg's *Darwinism Today* (1907) illustrates the sad state of Darwinian theory at the start of the twentieth century. Rather, it shows the solid support for Darwinism among American evolutionists. Kellogg was not blind to anti-Darwinian polemics but associated them specifically with French and German evolutionists, who in turn were reacting against neo-Darwinian overreach (Largent 2009, pp. 10–11). Based on a study of William Keith Brooks, Richard Nash similarly shows that Darwinism had support among more naturalists in the US than has been hitherto assumed (Nash 2015). Earlier we noted how de Vries's theory was explicitly advocated as Darwinian by researchers at the Station for Experimental Evolution. Nordenskiöld named only T. H. Morgan and his school among the American Mendelians and noted again how their theory is hybridized with the theory of selection (Nordenskiöld 1928, p. 615). If Darwinism had found itself in a precarious position in the United States in the decades after 1859, such persistence or growth in support is undoubtedly remarkable.

Another look at Kellogg's final chapter reveals the geographical insight that "there still exists, especially in England, thoroughgoing Darwinians" (Kellogg 1907, p. 389). With regards to Darwinism in medical circles, Fabio Zampieri similarly suggested that it was largely an "English" phenomenon (2009b, pp. 15–16). Writing for an English audience, Hubrecht suggested that *continental* Darwinians, had long been skeptical of *Wallace-ism*, except for Weismann, who was both continental and Wallace-ist (Hubrecht 1908). Bowler's own articles bear out the difficulty of showing Darwinism's decline in Britain. When comparing the American and British experiences, he observes how American anti-Darwinists had considerably more success from the start than in Britain, where people like Huxley and Lankester imprinted Darwinism upon the generations that followed (Bowler 1985). Bowler's article on Britain starting with the 1890s, in fact, mentions little scientific opposition but emphasizes rather religious and popular adversaries (Bowler 2004). The discrepancy suggests British Darwinist support (whether Wallace-ist or de Vriesian) for natural selection might not have been as eclipsed as it is supposed.

Unlike Germany, Darwinism elsewhere was not necessarily perceived as tied up in morphology. Hence, people stuck with forms of Darwinism even when morphological Darwinism was dealt a blow. Similarly, it was not tied into an anti-religious movement either. Darwin himself had drawn from Paley's natural theology in the construction of his theory. Richard England has emphasized how religious Oxford neo-Darwinians, like Edward Poulton and Frederick Dixey, believed support for Darwinian adaptation could reciprocally reaffirm the strength of such Christian undercurrents (2001, p. 271). The agnostic Romanes was supportive of Aubrey Moore's theological argument relying on *internal* rather than *external* Aristotelian logic and returned to theism on his deathbed (England 2001, pp. 278–281).

The rise of experimentalism, then, did not necessarily remove Darwinism from its significant foothold in the British world. In Richmond's discussion of the 1909 Cambridge celebrations of the centenary of Darwin's birth, dissenters' great effort to link their theories to Darwin is palpable, and the event left an imprint on the generation of students to come**.** Both Mendelism and mutationism were being increasingly looked upon as favorable and in line with Darwin's views (Richmond 2006, p. 470).

Provine seemed almost surprised at the speed at which the Synthesis occurred in England, but it is less surprising if there was already a solid basis to work on (Provine 1980, p. 333).

As Gould has noted, “national styles” seem to have influenced the development of evolutionary theory, and the centrality of natural selection after the “hardening” of the Synthesis reflects a long-held English tradition (Gould 1983, pp. 90–91). We must be wary of assuming that the supposed death of Darwinism was perceived the same way everywhere. Rather, Darwinism persisted in many places, although perhaps under different guises.

Conclusion

Wallace and other neo-Darwinians used a nascent eclipse narrative to delegitimize alternative approaches to Darwinism, especially those that did not privilege natural selection. Huxley, Mayr, and Bowler continued this historiographical tradition and can thus be described as contributing to a neo-Darwinian historiography. That is not to say there was no value in the eclipse narrative. Bowler’s use drew attention to a variety of non- and anti-Darwinian movements that had previously been neglected. Unfortunately, in hanging on to the neo-Darwinian view of Darwinism’s creative selectionist conception, many a scientist was branded anti-Darwinian when historically their relation to Darwinism was a lot more complicated.

This paper has tried to overcome this problem by utilizing *Darwinization* as an alternative frame. This framing describes the *process* by which individuals diverged from Darwin by moving into novel territory, yet sought to maintain compatibility with the master. If the rise of experimentalism challenged the role of the naturalist, it did not necessarily challenge the role of Darwinism. Studies of *qualitative* variation followed Darwin as much as studies of *quantitative variation*. Building on Beatty (2016), this analysis shows how mutationist and morphological Darwinians focused on the *contingency* of selection and the neo-Darwinians on the *creativity* of selection. Studies of non- and anti-Darwinians must emphasize that their antagonism could be directed to various fronts, depending on what Darwinism they were up against. In Germany, the fall of Haeckelian morphology was taken as Darwinism’s fall, even when people were still engaging with other elements of Darwin’s theory.

As our view of a united Darwinism or Modern Synthesis fails, the usefulness of the eclipse narrative becomes less clear. This critique of the eclipse narrative is not only aimed at conceptions that have been tied into a Synthesis Historiography; both advocates and detractors use the notion to simplify the complex dealings within the Synthesis. Through my study of de Vries, I hope to show that Stoltzfus and Cable’s claim—namely, that it was, in fact, the Synthesis that eclipsed new Mendelian-mutationist advances by advocating Darwinism—is an unnecessary simplification of what Darwin’s theory entailed (Stoltzfus and Cable 2014). Gould’s suggestion—that overcoming the Synthesis would finally overcome Darwinism’s reductionism—is similarly problematic (Gould 1982, p. 10). Instead, as James Moore has argued for quite some time, the *definition* of Darwinism itself must remain under historical scrutiny (Moore 1991).

The eclipse period was full of rich engagement with Darwinism, although some of that research engagement fell out of the scope of historiography as the neo-Darwinian narrative was taken up again and again. This acknowledgement will allow us to uncover both greater pluralism within, and more commonalities between, cultural groups in the history of evolutionary thought. In other words, the best way forward for the history of evolutionary theory is to eclipse the very notion of scientific eclipses. For only as a geographical phenomenon, where syntheses or eclipses are localized in specific places, does some value remain for that terminology. Hopefully, with that realization, new light can be shed on an understudied period.

Acknowledgements I wish to extend my heartfelt thanks to Peter Bowler, Diarmid Finnegan and Stuart Mathieson for their valuable feedback on earlier drafts of this paper, as well as their encouragement. As my PhD supervisor at Queen's University Belfast, Diarmid was particularly crucial in fostering what was at that point only the "germ" of an idea. Further thanks are to be extended to the two anonymous reviewers, as well as the editors, who gave very thorough feedback on earlier versions of this work. Any remaining errors are fully mine.

Funding This study was supported by Department for Education.

References

Adriaens, Pieter R., and Andreas De Block. 2010. The Evolutionary Turn in Psychiatry: A Historical Overview. *History of Psychiatry* 21 (2): 131–143.

Allen, Garland E. 1968. Thomas Hunt Morgan and the Problem of Natural Selection. *Journal of the History of Biology* 1 (1): 113–139.

Allen, Garland E. 1969. Hugo de Vries and the Reception of the "Mutation Theory." *Journal of the History of Biology* 2 (1): 55–87.

Allen, Garland E. 1979. Naturalists and Experimentalists: The Genotype and the Phenotype. *Studies in History of Biology* 3: 179–209.

Allen, Garland E. 1981. Morphology and Twentieth-century Biology: A Response. *Journal of the History of Biology* 14 (1): 159–176.

Amundson, Ron. 2005. *The Changing Role of the Embryo in Evolutionary Thought*. Cambridge, UK: Cambridge University Press.

Bartholomew, Matthew. 1975. Huxley's Defence of Darwin. *Annals of Science* 32 (6): 525–535.

Barton, Ruth. 2018. *The X-Club: Power and Authority in Victorian Science*. Chicago, IL and London: University of Chicago Press.

Beatty, John. 2006. Chance Variation: Darwin on Orchids. *Philosophy of Science* 73 (5): 629–641.

Beatty, John. 2010. Reconsidering the Importance of Chance Variation. In *Evolution: The Extended Synthesis*, ed. Gerd Müller and Massimo Pigliucci, 21–44. Cambridge, MA: MIT Press.

Beatty, John. 2016. The Creativity of Natural Selection? Part I: Darwin, Darwinism, and the Mutationists. *Journal of the History of Biology* 49 (4): 659–684.

Beatty, John. 2019. The Creativity of Natural Selection? Part II: The Synthesis and Since. *Journal of the History of Biology* 52 (4): 705–731.

Beatty, John, and Eric Cyr Desjardins. 2009. Natural Selection and History. *Biology & Philosophy* 24 (2): 231–246.

Bowler, Peter J. 1974. Darwin's Concepts of Variation. *Journal of the History of Medicine and Allied Sciences* 29 (2): 196–212.

Bowler, Peter J. 1976. Alfred Russel Wallace's Concepts of Variation. *Journal of the History of Medicine and Allied Sciences* 31 (1): 17–29.

Bowler, Peter J. 1983. *The Eclipse of Darwinism*. Baltimore, MD and London: John Hopkins University Press.

Bowler, Peter J. 1985. Scientific Attitudes to Darwinism in Britain and America. In *The Darwinian Heritage*, ed. David Kohn, 641–681. Princeton, NJ: Princeton University Press.
Bowler, Peter J. 1988. *The Non-Darwinian Revolution*. Baltimore, MD and London: John Hopkins University Press.
Bowler, Peter J. 1992. *The Eclipse of Darwinism*. Paperback. Baltimore, MD and London: John Hopkins University Press.
Bowler, Peter J. 2004. The Specter of Darwinism: The Popular Image of Darwinism in Early Twentieth-century Britain. In *Darwinian Heresies*, ed. Abigail Lustig, Robert J. Richards, and Michael Ruse, 48–68. Cambridge, UK: Cambridge University Press.
Bowler, Peter J. 2005. Revisiting the Eclipse of Darwinism. *Journal of the History of Biology* 38 (1): 19–32.
Bowler, P.J. 2009. The Eclipse of Pseudo-Darwinism? Reflections on Some Recent Developments in Darwin Studies. *History of Science* 47 (4): 431–443.
Bowler, Peter J. 2013. *Darwin Deleted*. Chicago, IL and London: University of Chicago Press.
Bowler, Peter J. 2017. Alternatives to Darwinism in the Early Twentieth Century. In *The Darwinian Tradition in Context*, ed. Richard Delisle, 195–217. Cham: Springer.
Burian, Richard M., Jean Gayon, and Doris Zallen. 1988. The Singular Fate of Genetics in the History of French Biology, 1900–1940. *Journal of the History of Biology* 21 (3): 357–402.
Butler, Samuel. 1880. *Unconscious Memory*. London: David Bogue.
Cain, Joe. 1993. Common Problems and Cooperative Solutions: Organizational Activity in Evolutionary Studies, 1936–1947. *Isis* 84 (1): 1–25.
Cain, Joe. 2009. Rethinking the Synthesis Period in Evolutionary Studies. *Journal of the History of Biology* 42 (4): 621–648.
Ceccarelli, D. 2019. Between Social and Biological Heredity: Cope and Baldwin on Evolution, Inheritance, and Mind. *Journal of the History of Biology* 52 (1): 161–194.
Darden, Lindley. 1976. Reasoning in Scientific Change: Charles Darwin, Hugo de Vries, and the Discovery of Segregation. *Studies in History and Philosophy of Science Part A* 7 (2): 127–169.
Darwin, Charles. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
Darwin, Charles. 1862. *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effect of Intercrossing*. London: John Murray.
Darwin, Charles. 1866. *On the Origin of Species by Means of Natural Selection, or the Preservation of FavouredRaces in the Struggle for Life*, 4th ed. London: John Murray.
Darwin, Charles. 1868a. *The Variation of Animals and Plants under Domestication*, vol. 1. London: John Murray.
Darwin, Charles. 1868b. *The Variation of Animals and Plants under Domestication*, vol. 2. London: John Murray.
Darwin, Charles. 1869. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 5th ed. London: John Murray.
Darwin, Charles. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
Darwin, Charles. 1872a. *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 6th ed. London: John Murray.
Darwin, Charles. 1872b. *The Expression of the Emotions in Man and Animals*. London: John Murray.
Davenport, Charles Benedict. 1909. Mutation. In *Fifty Years of Darwinism: Modern Aspects of Evolution: Centennial Addresses in Honor of Charles Darwin, before the American Association for the Advancement of Science, Baltimore, Friday, January 1, 1909*, ed. American Association for the Advancement of Science, 160–181. New York, NY: Henry Holt & Company.
De Bont, Raf. 2010. Schizophrenia, Evolution and the Borders of Biology: On Huxley et al.'s 1964 Paper in *Nature*. *History of Psychiatry* 21 (82, pt 2): 144–159.
Delisle, Richard G. 2009. The Uncertain Foundation of Neo-Darwinism: Metaphysical and Epistemological Pluralism in the Evolutionary Synthesis. *Studies in History and Philosophy of Biological and Biomedical Sciences* 40: 119–132.
Delisle, Richard G. 2017. From Charles Darwin to the Evolutionary Synthesis: Weak and Diffused Connections Only. In *The Darwinian Tradition in Context*, ed. Richard G. Delisle, 133–167. Cham: Springer International Publishing.
Dennert, Eberhard. 1904. *At the Deathbed of Darwinism*, trans. E.V. O'Hara and John H. Peschges. Burlington, IA: German Literary Board.

Depew, D.J., and B.H. Weber. 2011. The Fate of Darwinism: Evolution after the Modern Synthesis. *Biological Theory* 6 (1): 89–102.
Depew, David. 2017. Darwinism in the Twentieth Century: Productive Encounters with Saltation, Acquired Characters, and Development. In *The Darwinian Tradition in Context*, ed. Richard G. Delisle, 61–88. Cham: Springer International Publishing.
De Vries, Hugo. 1889. *Intracellulare Pangenesis*. Jena: G. Fischer.
De Vries, Hugo. 1901. *Die Mutationstheorie: Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich*, vol. 1. Leipzig: Veit & Comp.
De Vries, Hugo. 1903. *Die Mutationstheorie: Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich*, vol. 2. Leipzig: Veit & Comp.
De Vries, Hugo. 1904. *Species and Varieties, Their Origin by Mutation: Lectures Delivered at the University of California*. Chicago, IL: Open Court.
De Vries, Hugo. 1907a. *Plant-breeding: Comments on the Experiments of Nilsson and Burbank*. Chicago, IL: Open Court.
De Vries, Hugo. 1907b. New Principles in Agricultural Plant Breeding. *The Monist* 17: 209–219.
De Vries, Hugo. 1909. *The Mutation Theory: Experiments and Observations on the Origin of Species in the Vegetable Kingdom.* Vol. 1, trans, J.B. Farmer and A.D. Darbishire. Chicago, IL: Open Court.
De Vries, Hugo. 1910. *The Mutation Theory: The Origin of Varieties by Mutation.* Vol. 2, trans, J.B. Farmer and A.D. Darbishire. Chicago: Open Court.
De Vries, Hugo. 1914. Mutations in Heredity. In *The Book of the Opening of the Rice Institute*, vol. 2, ed. Rice Institute, 518–570. Houston, TX: Rice University.
De Vries, Hugo. 1919. The Present Position of the Mutation Theory. *Nature* 104: 213–214.
Di Gregorio, Mario A. 1982. The Dinosaur Connection: A Reinterpretation of T.H. Huxley's Evolutionary View. *Journal of the History of Biology* 15(3): 397–418.
Eldridge, Niles. 1985. *Unfinished Synthesis*. Oxford: Oxford University Press.
Endersby, Jim. 2013. Mutant Utopias: Evening Primroses and Imagined Futures in Early Twentieth-century America. *Isis* 104 (3): 471–503.
England, Richard. 2001. Natural Selection, Teleology, and the Logos: From Darwin to the Oxford Neo-Darwinists, 1859–1909. *Osiris* 16: 270–287.
Finnegan, D.A. 2008. The Spatial Turn: Geographical Approaches in the History of Science. *Journal of the History of Biology* 41 (2): 369–388.
Finnegan, Diarmid. 2010. Darwin, Dead and Buried? *Environment and Planning A* 42 (2): 259–261.
Gayon, Jean. 1990. Critics and Criticisms of the Modern Synthesis: The Viewpoint of a Philosopher. *Evolutionary Biology* 24: 1–49.
Gayon, Jean. 1998. *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection*. Cambridge, UK: Cambridge University Press.
Gayon, Jean, and Philippe Huneman. 2019. The Modern Synthesis: Theoretical or Institutional Event? *Journal of the History of Biology* 52 (4): 519–535.
Geison, G.L. 1969. Darwin and Heredity: The Evolution of his Hypothesis of Pangenesis. *Journal of the History of Medicine and Allied Sciences* 24 (4): 375–411.
Gould, Stephen J. 1980. Is a New and General Theory of Evolution Emerging? *Paleobiology* 6: 119–130.
Gould, Stephen J. 1982. Darwinism and the Expansion of Evolutionary Theory. *Science* 216 (4544): 380–387.
Gould, Stephen J. 1983. The Hardening of the Modern Synthesis. In *Dimensions of Darwinism*, ed. Marjorie Grene, 71–93. Cambridge, UK: Cambridge University Press.
Gould, Stephen J. 2002. *The Structure of Evolutionary Theory*. Cambridge, MA and London: Harvard University Press.
Haeckel, Ernst. 1868. *Natürliche Schöpfungsgeschichte*. Berlin: Georg Reimer.
Hale, Piers J. 2015. Rejecting the Myth of the Non-Darwinian Revolution. *Victorian Review* 41 (2): 13–18.
Harwood, Jonathan. 1993. *Styles of Scientific Thought: The German Genetics Community, 1900–1933*. Chicago, IL and London: University of Chicago Press.
Holterhoff, Kate. 2014. The History and Reception of Charles Darwin's Hypothesis of Pangenesis. *Journal of the History of Biology* 47 (4): 661–695.
Hoquet, Thierry. 2013. The Evolution of the *Origin*. In *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, ed. M. Ruse, 158–164. Cambridge, UK: Cambridge University Press.
Hubrecht, Ambrosius. 1904. Hugo de Vries' Theory of Mutations. *Popular Science Monthly* 65: 205–223.
Hubrecht, Ambrosius. 1908. Darwinism *versus* Wallaceism. *Contemporary Review* 93: 629–634.

Hull, David L. 1985. Darwinism as a Historical Entity: A Historiographic Proposal. In *The Darwinian Heritage*, ed. David Kohn, 773–812. Princeton, NJ: Princeton University Press.
Huxley, Julian. 1942. *Evolution: The Modern Synthesis*. London: George Allen & Unwin Limited.
Huxley, Julian. 1946. *UNESCO: Its Purpose and Its Philosophy*. Washington, D.C.: Public Affairs Press.
Huxley, Julian. (1945) 1947a. The Vindication of Darwinism. In *Evolution and Ethics, 1893–1943*, ed. Julian Huxley, 153–176. London: The Pilot Press.
Huxley, Julian. (1943) 1947b. Evolutionary Ethics. In *Evolution and Ethics*, ed. Julian Huxley, 103–42. London: The Pilot Press.
Huxley, Thomas Henry. 1860a. Darwin On the Origin of Species. *Westminster Review* 17: 541–570.
Huxley, Thomas Henry. 1877. *American Addresses with a Lecture on the Study of Biology*. London: Macmillan and Co.
Huxley, Thomas Henry. (1871) 1893a. Mr Darwin's Critics. In *Collected Essays: Darwiniana*, ed. T. H. Huxley, 120–186. London: Macmillan.
Huxley, Thomas Henry. (1864) 1893b. Criticisms on "The Origin of Species." In *Collected Essays: Darwiniana*, ed. T. H. Huxley, 80–106. London: Macmillan.
Huxley, Thomas Henry. (1869) 1893c. The Genealogy of Animals. In *Collected Essays: Darwiniana*, ed. T. H. Huxley, 107–119. London: Macmillan.
Huxley, Thomas Henry. (1878) 1893d. Evolution in Biology. In *Collected Essays: Darwiniana*, ed. T. H. Huxley, 187–226. London: Macmillan.
Huxley, Thomas Henry. (1888) 1893e. Obituary for Charles Robert Darwin. In *Collected Essays: Darwiniana*, ed. T. H. Huxley, 253–302. London: Macmillan.
Huxley, Thomas Henry. (1860) 1896. The Origin of Species. In *Darwiniana,* ed. Thomas Henry Huxley, 22–79. New York: D. Appleton and Company.
Huxley, Thomas Henry. (1868) 1901a. On the Animals Which Are Most Nearly Intermediate between Birds and Reptiles. In *The Scientific Memoirs of Thomas Henry Huxley.* Vol. 3, ed. Michael Foster and Edwin Ray Lankester, 303–313. London: Macmillan and Company.
Huxley, Thomas Henry. (1870) 1901b. The Anniversary Address of the President. In *The Scientific Memoirs of Thomas Henry Huxley.* Vol. 3, ed. Michael Foster and Edwin Ray Lankester, 510–550. London: Macmillan and Company.
Huxley, Thomas Henry. (1876) 1902a. On the Evidence as to the Origin of Existing Vertebrate Animals. In *The Scientific Memoirs of Thomas Henry Huxley.* Vol. 4, ed. Michael Foster and Edwin Ray Lankester, 163–187. London: Macmillan and Company.
Huxley, Thomas Henry. (1880) 1902b. On the Application of the Laws of Evolution to the Arrangement of the *Vertebrata*, and More Particularly of the *Mammalia*. In *The Scientific Memoirs of Thomas Henry Huxley.* Vol. 4, ed. Michael Foster and Edwin Ray Lankester, 457–473. London: Macmillan and Company.
Jenkin, Fleming. 1867. The Origin of Species. *North British Review* 46 (92): 277–318.
Kellogg, Vernon L. 1907. *Darwinism Today.* New York, NY: Henry Holt and Company.
Kelly, Alfred. 1981. *The Descent of Darwin*. Chapel Hill, NC: University of North Carolina Press.
Kingsland, S.E. 1991. The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900–1912. *Isis* 82 (3): 479–509.
Lankester, E. Ray. (1888) 1890. *The History and Scope of Zoology*. In *The Advancement of Science*, ed. Edwin Ray Lankester, pp. 287–384. London: Macmillan and Co.
Lankester, E.R. 1888. Functionless Organs. *Nature* 38 (981): 364–364.
Lankester, E. Ray. 1907. *The Kingdom of Man*. London: Archibald Constable.
Largent, M.A. 2009. The So-called Eclipse of Darwinism. *Transactions of the American Philosophical Society* 99 (1): 3–21.
Largent, Mark A. 2013. Darwinism in the United States, 1859–1930. In *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, ed. Michael Ruse, 226–234. Cambridge, UK: Cambridge University Press.
Levit, Georgy S., and Kay Meister. 2006. The History of Essentialism vs. Ernst Mayr's "Essentialism Story": A Case Study of German Idealistic Morphology. *Theory in Biosciences* 124 (3–4): 281–307.
Liepman, Helen P. 1981. The Six Editions of the "Origin of Species": A Comparative Study. *Acta Biotheoretica* 30 (3): 199–214.
Limoges, Camille. 1976. Natural Selection, Phagocytosis, and Preadaptation: Lucien Cuénot, 1886–1901. *Journal of the History of Medicine and Allied Sciences* 31 (2): 176–214.

Livingstone, David N. 2003. *Putting Science in Its Place: Geographies of Scientific Knowledge*. Chicago, IL: University of Chicago Press.
Loison, Lauren. 2011. The Notions of Plasticity and Heredity among French Neo-Lamarckians (1880–1940): From Complementarity to Incompatibility. In *Transformations of Lamarckism*, eds. Snait B. Gissis and Eva Jablonka, 67–77.Cambridge, MA and London: MIT Press.
Lustig, Abigail J. 2002. Erich Wasmann, Ernst Haeckel, and the Limits of Science. *Theory in Biosciences* 121 (3): 252–259.
Lyons, Sherrie L. 1995. The Origins of T. H. Huxley's Saltationism: History in Darwin's Shadow. *Journal of the History of Biology* 28 (3): 463–494.
Marchant, James. 1916. The Complete Extant Correspondence between Wallace and Darwin (1857–81). In *Alfred Russel Wallace: Letters and Reminiscences,* ed. James Marchant. Vol. 1: 127–320. London: Cassell and Company.
Mayr, Ernst. 1980. Prologue: Some Thoughts on the History of the Evolutionary Synthesis. In *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine, 1–48. Cambridge, MA: Harvard University Press.
Mayr, Ernst. 1982. *The Growth of Biological Thought*. Cambridge, MA and London: The Belknap Press of Harvard University Press.
Mayr, Ernst. 1984. What Is Darwinism Today? *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1984 (2): 145–156.
Mayr, Ernst. 1991. *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought*. Cambridge, MA: Harvard University Press.
Mayr, Ernst. 1998. Preface. In *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine, ix–xiv. Cambridge, MA: Harvard University Press.
Meldola, Raphael. 1888. Lamarckism Versus Darwinism. *Nature* 38 (982): 388–389.
Mivart, St. George John. 1871. *The Genesis of Species*. London: Macmillan.
Moore, James. 1991. Deconstructing Darwinism: The Politics of Evolution in the 1860s. *Journal of the History of Biology* 24 (3): 353–408.
Morgan, T.H. 1903. *Evolution and Adaptation*. New York, NY: Macmillan Company.
Morgan, T.H. 1918. Concerning the Mutation Theory. *Scientific Monthly* 6 (5): 385–405.
Nash, Richard. 2015. William Keith Brooks and the Naturalist's Defense of Darwinism in the Late-nineteenth Century. *History and Philosophy of the Life Sciences* 37 (2): 158–179.
Nordenskiöld, Erik. 1928. *The History of Biology*. Trans. Leonard Bucknall Eyre. New York: Tudor Publishing.
Orzack, S.H. 1981. The Modern Synthesis is Partly Wright. *Paleobiology* 7 (1): 128–131.
Pauly, P. J. 1982. Samuel Butler and His Darwinian Critics. *Victorian Studies* 25 (2): 161–180.
Pfeifer, Edward J. 1965. The Genesis of American Neo-Lamarckism. *Isis* 56 (2): 156–167.
Poulton, E.B. 1888a. Dr. Romanes' Article in the Contemporary Review for June. *Nature* 38(978): 295–296.
Poulton, E. B. 1888b. Lamarckism Versus Darwinism. *Nature* 38 (982): 388–389.
Poulton, Edward Bagnall. 1896. *Charles Darwin and the Theory of Natural Selection*. London: Cassell & Co.
Poulton, E.B. 1909. *Charles Darwin and the Origin of Species: Addresses, etc., in America and England in the Year of the Two Anniversaries*. London: Longmans, Green, and Company.
Provine, William B. 1980. England. In *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine, 329–334. Cambridge, MA: Harvard University Press.
Provine, William B. 1992. Progress in Evolution and Meaning in Life. In *Julian Huxley: Biologist and Statesman of Science: Proceedings of a Conference held at Rice University 25–27 September 1987*, eds. C.K. Waters and A. Van Helden, 193–222. Houston, TX: Rice University Press.
Provine, William B. 2001. *The Origins of Theoretical Population Genetics: With a New Afterword*. Chicago, IL and London: University of Chicago Press.
Radick, Gregory. 2010. Darwin's Puzzling Expression. *Comptes Rendus Biologies* 333 (2): 181–187.
Rádl, Emanuel. 1909. *Geschichte der Biologischen Theorien*. Leipzig: Verlag von Wilhelm Engelman.
Rádl, Emanuel. 1930. *The History of Biological Theory.* Trans. E.J. Hatfield. London: Oxford University Press.
Reif, W.E., Thomas Junker, and Uwe Hoßfeld. 2000. The Synthetic Theory of Evolution: General Problems and the German Contribution to the Synthesis. *Theory in Biosciences* 119 (1): 41–91.

Richards, Robert J. 2005. Ernst Haeckel and the Struggles over Evolution and Religion. *Annals of the History and Philosophy of Biology* 10: 89–115.
Richards, Robert J. 2008. *The Tragic Sense of Life*. Chicago, IL and London: The University of Chicago Press.
Richards, Robert J. 2013. The German Reception of Darwin's Theory, 1860–1945. In *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, ed. Michael Ruse, 235–243. Cambridge, UK: Cambridge University Press.
Richmond, Marsha L. 2006. The 1909 Darwin Celebration: Reexamining Evolution in the Light of Mendel, Mutation, and Meiosis. *Isis* 97 (3): 447–484.
Roll-Hansen, Nils. 1989. The Crucial Experiment of Wilhelm Johannsen. *Biology and Philosophy* 4 (3): 303–329.
Roger, Jacques. 1985. Darwinism Today (Commentary). In *The Darwinian Heritage*, ed. David Kohn, 813–823. Princeton, NJ: Princeton University Press.
Romanes, G. J. 1881a. Unconscious Memory. *Nature* 23 (587): 285–287.
Romanes, G. J. 1881b. Mr. Butler's "Unconscious Memory." *Nature* 23 (589): 335–336.
Romanes, George J. 1887. The Factors of Organic Evolution. *Nature* 36: 401–407.
Romanes, George J. 1888a. Dr. Romanes's Article in the "Contemporary Review." *Nature 38*(981): 364–364.
Romanes, George J. 1888b. Lamarckism versus Darwinism. *Nature* 38 (983): 413.
Romanes, George J. 1888c. Natural Selection and the Origin of Species. *Nature* 39 (999): 173–175.
Romanes, George J. 1889. Mr. Wallace on Darwinism. *Science* 14 (343): 150–155.
Romanes, George John. 1895. *Darwin, and After Darwin*, vol. 2. London: Longmans, Green and Co.
Romanes, Ethel. 1896. *The Life and Letters of George John Romanes*. London: Longmans, Green, and Co.
Ruse, Michael. 2009. *Monad to Man: The Concept of Progress in Evolutionary Biology*. Paperback. Cambridge, MA and London, England: Harvard University Press.
Shull, George H. 1905. Species and Varieties: Their Origin by Mutation. *Torreya* 5 (5): 89–93.
Shull, George H. 1907. Importance of the Mutation Theory in Practical Breeding. *Proceedings of the American Breeders' Association* 3: 60–67.
Smocovitis, V. Betty. 1992. Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology. *Journal of the History of Biology* 25 (1): 1–65.
Stebbins, G. Leyard, and Fransisco J. Ayala. 1981. Is a New Evolutionary Synthesis Necessary? *Science* 213 (4511): 967–971.
Stoltzfus, Arlin, and Kele Cable. 2014. Mendelian-mutationism: The Forgotten Evolutionary Synthesis. *Journal of the History of Biology* 47 (4): 501–546.
Theunissen, Bert. 1994. Closing the Door on Hugo de Vries' Mendelism. *Annals of Science* 51 (3): 225–248.
Wallace, A.R., 1870a. *Contributions to the Theory of Natural Selection: A Series of Essays*. London: Macmillan and Company.
Wallace, A.R. 1870b. Natural Selection—Mr. Wallace's Reply to Mr. Bennet. *Nature* 1870–71 (3): 49–50.
Wallace, Alfred Russel. 1889. *Darwinism*. London: MacMillan and Co.
Wallace, Alfred Russel. 1908a. The Present Position of Darwinism. *Contemporary Review* 93: 129–141.
Wallace, Alfred Russel. 1908b. Darwinism *Versus* Wallaceism. *Contemporary Review* 93: 716–717.
Weismann, August. 1889. *Essays upon Heredity and Kindred Biological Problems.* Trans. E.B. Poulton, S. Schönland, and A.E. Shipley. Oxford: Clarendon Press.
Weismann, August. 1904. *The Evolution Theory*, 2nd ed. 2 vols. Trans. J. A. Thomson and M. R. Thomson. London: Edward Arnold
Winsor, Mary P. 2006. The Creation of the Essentialism Story: An Exercise in Metahistory. *History and Philosophy of the Life Sciences* 28: 149–174.
Winsor, Mary P. 2013. Darwin and Taxonomy. In *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, ed. Michael Ruse, 72–79. Cambridge: Cambridge University Press.
Winther, Rasmus G. 2000. Darwin on Variation and Heredity. *Journal of the History of Biology* 33 (3): 425–455.
Zampieri, Fabio. 2009a. Medicine, Evolution, and Natural Selection: An Historical Overview. *The Quarterly Review of Biology* 84 (4): 333–334.
Zampieri, F. 2009b. Origins and History of Darwinian Medicine. *Humana Mente* 9: 13–38.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.