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CLASSICS IN BIOLOGICAL THEORY

Revisiting George Gaylord Simpson's "The Role of the Individual in Evolution" (1941)

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Abstract
"The Role of the Individual in Evolution" is a prescient yet neglected 1941 work by the 20th century's most important paleontologist, George Gaylord Simpson. In a curious intermingling of explanation and critique, Simpson engages questions that would become increasingly fundamental in modern biological theory and philosophy. Did individuality, adaptation, and evolutionary causation reside at more than one level: the cell, the organism, the genetically coherent reproductive group, the social group, or some combination thereof? What was an individual, anyway? In this introduction, we highlight two points in a wider historical context. First, recognizing the political context of Simpson's writing profoundly deepens our understanding of the development of his science as the Modern Evolutionary Synthesis infused biology. Second, this story illuminates the emergence of debates around what would eventually come to be called multilevel selection theory. The organism-centered concept of biological individuality defended by Simpson is situated in relation to the then-emerging Synthesis, in which he was a renowned player, and also in relation to the views he opposed: the "metaphysical" ideas of paleontologists such as Henry Fairfield Osborn, who claimed that some evolutionary trends derived from potentialities already implanted in the germplasm; and the organicist ideas of Ralph W. Gerard and the Chicago School of ecologists, which he derided as all too congenial to totalitarianism. We find parallels between the ways that Simpson thought then about human individuality under totalitarianism and the way he thought about individuality in evolution; not that any causal relationship linked the two, but that commonalities of hierarchical structure exist between single entities and groups in both instances. We then trace the subsequent development of Simpson's political and philosophical takes on the role of the individual in evolution through the 1960s and lightly sketch out the later fate of the organicist ideas of the Chicago School. Simpson's paper, originally published in the *Journal of the Washington Academy of Sciences* (31:1–20), is available as supplementary material in the online version of this article, as part of the "Classics in Biological Theory" collection.

Keywords Biological individuality · Democracy · Evolutionary synthesis · Multilevel selection · George Gaylord Simpson · Totalitarianism

Introduction

Some have called him the most influential paleontologist of the 20th century. George Gaylord Simpson (1902–1984), together with Julian Huxley, Ernst Mayr, and Theodosius Dobzhansky, helped transform the theoretical foundations of the neo-Darwinian evolutionary paradigm into what Huxley named the Modern Synthesis. In this union of biological subdisciplines around evolution, Simpson's key contribution was to connect the dynamics of fossil history with systematics and field population genetics. Early on, his *Quantitative Zoology* (1939, with Anne Roe) stimulated decades of dramatic increase in the use of statistics across biological disciplines, aiding what Mayr later called "population thinking"—recognition of quantitative variation among closely related organisms and their ecology, population structure, biogeography, and a reinterpretation of species as evolving populations instead of a systematist's reference to invariant "types" (Hagen 2003). By 1935, Simpson had begun work on his foundational *Tempo and Mode in Evolution* (1944; Olson 1991). Subsequently inspired by Dobzhansky's 1937

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Fig. 1 George Gaylord Simpson portrait with *The Meaning of Evolution*, 1950. American Museum of Natural History Library, Image #2A858 (reprinted with permission)

Genetics and the Origin of Species, Simpson offered a new vision of rates and patterns of evolutionary change, of selection as a creative factor as well as a negative one, and he set motifs in paleontology and evolutionary biology that have endured through today (Fitch and Ayala 1995; Liow 2004; Hopkins and Lidgard 2012; Sepkoski 2019). For this work and its successors, as well as his massive quantity of empirical work in vertebrate paleontology, he has been widely recognized among scientists as a pivotal figure in 20th-century evolutionary theory. Simpson's reach extended beyond the scientific community. Not long after finishing *Tempo and Mode*, he became known to a broader audience via his acclaimed popular work *The Meaning of Evolution* (1949; see Fig. 1). With this and later writings, he would become an integral part of a movement dubbed by Huxley "evolutionary humanism," which offered a liberal, secular vision of humanity's role in nature based on evolution (Simpson 1949, 1964, 1966, 1969; Smocovitis 2016).

In addition to his books, Simpson published hundreds of articles over his career. "The Role of the Individual in Evolution," introduced here,[1] is not famous among them. Yet we think it should not be lost to history, for it speaks to issues of evolutionary theory, biological individuality, and the politics and philosophy of science that have continued to resonate since its original appearance in 1941. After outlining the article itself in its immediate historical context, we sketch its implications for both science and its sociopolitical context as they intertwined in the 1930s and 40s, developed further in the postwar period, and take on renewed significance today.

The Paper and Its Immediate Context

In November 1940, a 38-year-old Simpson spoke before the Paleontological Society of Washington, including scientists of the Smithsonian Institution's Natural History Museum. Two months later, the presentation was published in the *Journal of the Washington Academy of Sciences*, the mouthpiece of a consortium of scientific societies centered in Washington, D.C., and dedicated to exposing scientists, both locally and nationally, to current research. The audience, then, was both astute and influential. Simpson's presentation illuminated a classic, multipronged question: what constituted an "individual" in biology—a unified functional whole or something more complicated; whether individuals existed above the organismal level; and why such a definition was important (Child 1915; Bouchard and Huneman 2013; Lidgard and Nyhart 2017a; Baedke 2019). His answer offered a potent mix of juxtaposed definitions and examples of biological individuality from cell-organism relationships to eusocial insects, evolution and emergence at successive hierarchical levels, cooperation and subservience, politics and totalitarianism.

But just what compelled this paper? Simpson addressed both what he saw as the correct application of individuality concepts in biological science and the inappropriate, even dangerous, metaphorical extrapolation of emergent individuality from biology to human society (Mitman 1992; Keulartz 1998; see also Winther 2005). He constructed his narrative in sections, each building on the messages of preceding ones: kinds and degrees of individuality as seen in nature; the roles of individuals and their variation under Darwinian selection; the metaphysical, teleological underpinnings of evolutionary determinism; the centrality of time to dynamic concepts of individuals and groups; and the analogy between biological individuals and society, especially fraught with the advent of totalitarianism. Much was at stake.

Simpson (1941, p. 1) opened the introduction with his central biological theme: "Whatever happens in organic evolution, or indeed within the whole realm of the biological sciences, happens to an individual." He recognized that there are different categories and degrees of individuality, and that evolution among lineages has generated decreases as well as increases in individuality (Fig. 2). His examples told of a hierarchy of individuality generated through time. Comparing a unicellular organism to a cell in a metazoan, he explained how in the latter case more individuality is now at the level of the metazoan, with its cells having lost nearly all the autonomy they had as independent organisms. In the

[1] Simpson's paper is available as supplementary material in the online version of this article, as part of the journal's "Classics in Biological Theory" collection.

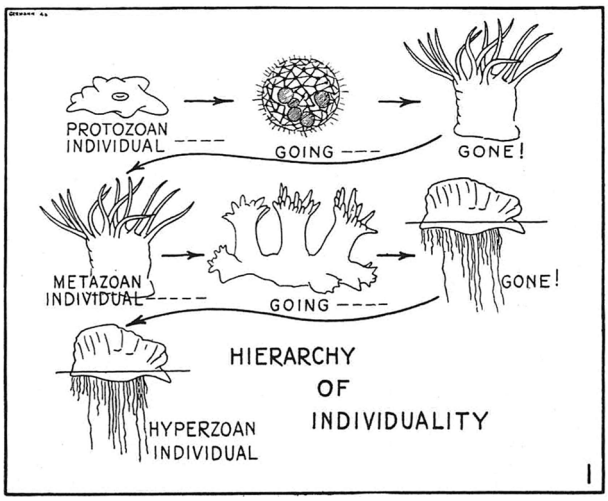

Fig. 2 "Hierarchy of Individuality" (Fig. 1.1 from original paper). Acknowledging the difficulties of a simple definition of the term "individual," Simpson uses the first figure in his 1941 paper to show how "There has been evolution toward more and toward less individuality" (p. 1). Comparing a fully individual protozoan to a colony of the chlorophyte *Volvox*, and subsequently a solitary cnidarian, he infers that the single cell's individuality is gradually lost and that the metazoan exhibits individuality on a different level. Then comparing multiple uniform polyps in colonial cnidarians and subsequently the functionally and structurally differentiated polyps in the siphonophore *Physalia*, yet another level is reached. Polyp individuality is diminished in favor of what he terms "hyperzoan individuality." (Reprinted with permission from the *Journal of the Washington Academy of Sciences*)

siphonophore *Physalia*, where the zooids display a division of labor, colony members "have almost entirely abdicated their individualities" (1941, p. 1). However, he cautioned, analogues of this kind of emergent colony-level individuality had seldom evolved among metazoan taxa and were not in evidence among vertebrates, including humans and their societies.[2]

The first section—"The Individual, Darwinism, and Genetics"—continued the biological theme, arguing that natural selection is mechanistically operative on individual organisms and population variation among them, not on the group or taxon as a whole (as paleontologists were wont to assume, if they accepted natural selection at all): "The species is a sum or collectivity of individuals, and it is an entity only in this sense, not in the sense of having a sort of superindividuality" (Simpson 1941, p. 4). Belonging to a group conferred an advantage to individuals in the sense that benefits are conferred by reproduction and continued group survival. Secondly, following directly on Darwin (1859, p. 45), Simpson argued that hereditary variation among individuals is itself crucial. He stressed that natural selection is not merely a pruning process. Along with instigating the death of less fit individuals, selection preserves the fitter individuals with adaptive mutations or recombinations, thus also preventing the extinction of species. Even where such variation appears to yield altruistic, self-sacrificing individuals, this was a result of the mechanistic processes of Darwinian evolution rather than intent, in contrast to altruism in humans. In this way, Simpson articulated a vision of evolution operating on individual organisms that would become central to the Modern Evolutionary Synthesis that was then emerging.

In section two, "The Individual and Evolutionary Fatalism," and three, "The Individual and the Fourth Dimension," Simpson railed against what he called evolutionary determinism. He demanded that scientists adopt a dynamic concept of individuals and of groups. Neither individuals nor groups should be understood as static entities. Characterizing teleological reasoning as "evolutionary fatalism," he rejected it as metaphysical and antithetical to the accepted mechanistic empirical understanding of Darwinian evolution. He scorned orthogenesis, the general idea that evolution proceeds through internally driven, linear progressive trends—in particular fingering "aristogenesis," an updated version of orthogenesis developed by paleontologist and eugenics advocate Henry Fairfield Osborn, his former boss at the American Museum of Natural History, who had died in 1935. Osborn (1931, 1934) had dismissed the importance of random genetic mutations and their selection as sufficient to account for evolutionarily significant change. He argued instead that, "Nature does not waste time or effort with chance or fortuity" (1931, p. 60) but seeded the germplasm with potentialities for improvement that are realized over geological time. (For an unusually sympathetic portrait of Osborn that clarifies his oft-changing views on evolution, see Ceccarelli 2021.) To Simpson, predetermined trends and seemingly vitalistic explanations like Osborn's simply could not be justified, when instead they could be explained in mechanistic genetic terms. Simpson further criticized older taxonomic approaches that understood higher-level groups as defined only by fixed characters shared by all individual members, as where a named taxonomic group is defined by an abstraction, a reference only to a stagnant single "type." Rather, statistical variation of characters among individual members should collectively characterize a group: "the group is best definable as a collection of individuals and not as an abstraction of the nonindividual" (Simpson 1941, p. 13). It was this variation and its temporal change over

[2] Eusociality, in which only a few member organisms in a closely-related colony are involved in reproduction, was thought to occur only among certain insects (e.g., bees, ants, termites) until it was reported in naked mole rats by Jennifer Jarvis (1981). Maximum expression of vertebrate eusociality appears to be restricted to two species of mole rats, but lesser forms of cooperative breeding occur in other mammalian and avian species that form social groups.

many successions of different individuals that was important evolutionarily, as a group "achieves adaptation and progresses only in the sense that the individuals composing it do so" (1941, p. 13).

In the final section, "The Individual and Totalitarianism," Simpson brought his biological arguments to bear in a grave warning to fellow scientists and to society. He took aim at the University of Chicago physiologist Ralph Gerard, a close ally of Alfred E. Emerson, W. C. Allee, and others in the famed group of “Chicago Ecologists.” This group played a major role in ushering in the modern era of population biology in the 1930s and 40s and community ecology in the 1950s and 1960s, particularly through the seminal publication *Principles of Animal Ecology* (Allee et al. 1949). The Chicago Ecologists pursued research drawing heavily on organicist, sometimes anti-mechanist views of the 1920s and 30s among members of the Vienna Circle and American biologists such as Charles M. Child and William E. Ritter (Mitman 1992; Winther 2005; Nicholson and Gawne 2015; Esposito 2017). Gerard was a brilliant neurophysiologist whose work synthesized observations from many disciplines. Emerson was an expert on social insects who became the world authority on the classification and ecology of termites. Separately and together, they were important to establishing a number of foundational, though at times controversial, themes that have carried into modern biology: a basic hierarchical scaffold of levels of organization and integration found in living nature, multilevel adaptation and selection, emergent evolution and its relations to group selection, the superorganism concept, and more (e.g., Emerson 1939, 1946; Gerard 1940a, b, 1942, 1957, 1958; Allee et al. 1949). When Simpson wrote his address, Gerard had just recently (1940a, b) elaborated his belief in ever-increasing evolutionary integration, in which cooperation, altruistic self-sacrifice, and subordination to the group were more advantageous to the biological community than competition. Gerard recommended the perceived benefits of this path for human society.

Applying biosocial holism in the human realm, however, ran into an increasingly apparent obstacle: totalitarianism. By late 1940, Nazi Germany had conquered most of Europe, tensions were rising over Japan's imperialism, and Lysenko had already begun his anti-Mendelian crusade under Stalin’s leadership. All three trends were beginning to be lumped together as a collective threat to individual freedom, and in particular, the intellectual freedom associated with science (Hollinger 1996; Wolfe 2018). The Chicago Ecologists’ leap from a version of scientific naturalism that took part-whole relations of integration and division of labor within an organism or an insect colony and extrapolated them to the human social realm fell afoul of this growing antipathy toward totalitarianism and Cold War communism (Mitman 1992).

In 1941, Simpson grasped the nettle, challenging the legitimacy of such hierarchical analogizing and its extrapolation to humanity. While he did describe the appearance of hierarchical levels of organization and degrees of individuality in living nature, he adamantly denied any top-down directive process or evolutionary causation in what he saw as two faulty inferences: Gerardian integration of higher-level groups and the metaphysical workings of orthogenesis. In organic evolution and the whole realm of biological sciences, it all "happens to an individual" (Simpson 1941, p. 1), that is, individual organisms. To be sure, these interactions had significant population-level effects, but populations needed to be treated as collectivities, not as integrated higher-level individuals themselves.

Gerard (1940a, b) had contended that organisms and human societies—“epiorganisms” in his terminology—are hierarchical homologues: both are spatiotemporally bounded individuals. Both were manifestations of his metaphysical concept of the "org," an inclusive or extended sense of organism existing at multiple organizational levels. Part-whole and part-part mechanisms of integration within the org, undergoing development or evolution, lead naturally to increasing dominion of the higher-level org, with advantage to all. By analogy, the well-being of a society (higher-level org) was paramount, and individuals in a society were subordinate units.

Simpson wouldn't have it. Comparing the individual within society to a cell or organ within a multicellular organism was no more than a descriptive, observational metaphor of parts to wholes without any predictive value or scientific basis; the "two relationships involve entirely different orders of things and do not belong in the same field of thought" (Simpson 1941, p. 18). If one nevertheless accepted the organism-society analogy and evolution toward greater integration, Simpson argued, then the inevitable outcome was increasing integration and specialization of individuals (people), entailing the loss of individual freedom and variability (scope for change) in the service and at the direction of the whole (the state): a "totalitarian ideal." The logic of this analogy was clear, and it failed in light of the role of the individual in evolution. Gerard's conception of the causal org had no more scientific legitimacy than did Osborn's aristogenesis. For Simpson, Gerard's distinction between good integrationism and bad totalitarianism was illusory, as seen in the many different totalitarian regimes currently at war. The social group or totalitarian state cannot be the source of variation or the level upon which natural selection acts; those are the roles of the individual. In this spirit Simpson concluded that individuals, free in a democratic society, are the true source of variation and human progress. To underscore the patriotic element, in the published version of his address he included as epigraphs to each section quotations from Walt Whitman’s poem “By Blue Ontario’s Shores.”

Though the quoted lines stressed only the importance of individuals, the poem itself (newly republished in Whitman 1940) emphasized America's historical struggle for democracy and freedom.

Historical Implications and Significance

Why is this somewhat odd lecture-turned-article worth reading today? We suggest that it is illuminating both historically and for the present. It offers a touchstone for our understanding of the development of the Modern Evolutionary Synthesis in relation to politics in the years around World War II. It also illuminates how ideas about biological part-whole relations, individuality, hierarchy, and the general processes of evolution and their applications to humans, crossed over between scientific and political spheres during and after World War II, with consequences that linger today.

As important as Simpson was in his lifetime, his intellectual development has received considerably less attention than the other leaders of the Synthesis, including surprisingly little analysis of the development of his seminal book *Tempo and Mode in Evolution* (1944; Laporte 2000; Cain 2009; Sepkoski 2019). In the present article, we see an early articulation of the key concepts of that book—published in 1944 but already well in process by late 1940 (Simpson 1953, p. ix). Regarding evolutionary "tempo," in the 1941 article, Simpson digressed from his main topic of individuality to offer a paragraph on rapid evolution and its theoretical connection to the small size of populations, in contrast to larger populations that evolve more slowly—an insight borrowed from population geneticists. He pointed out to his paleontological audience that their fossil specimen collections, especially if they were "rich in individuals," probably represented larger groups that remain more stable and change only slowly over time. "Such groups do, of course, give legitimate evidence of *some* of the *modes of evolution*," he wrote (1941, p. 6; emphasis added), but these are unlikely to be the only ones. Thus paleontologists' generalizations about linear trends in evolution (read Osborn's orthogenesis) reflected the limits of their evidence (and their analytical methods; see Simpson 1937) rather than the varied processes at work in producing novelty. While multiple tempos and modes of evolution made only a brief appearance in this paper, they were crucially connected to Simpson's thinking about the centrality of individuals in the story of evolution. Implicitly, the connection he made between individuals and species evolution points to what would be a fundamental element of the Modern Synthesis, and his own contribution to it: the claim that the higher-level, long-term evolutionary trends that were the main concern of the paleontologist should be interpreted as consistent with processes operating at the level of individuals and populations, and indeed, derived from those processes. It is worth noting, though, that the distinction Simpson made in 1941, between rapid evolution by small populations and gradual evolution as more characteristic of large populations, would by 1944 grow into a major argument. Although many and perhaps most evolutionists at this time distinguished between micro- (subspecific) evolution and macroevolution (evolution at and above the species level),[3] Simpson felt compelled further to distinguish "mega-evolution"—the origin of discontinuity at the higher levels of class, order, and family, the levels most visible to paleontologists, and least addressed empirically by neontologists. Lower-level macroevolution (of species and genera) was typically a gradual process of larger populations. Mega-evolution, Simpson hypothesized, could result from extremely rapid evolution among small populations, often triggered by a major environmental change—a process that by the end of the book he would work into the more general mode he called "quantum" evolution (Simpson 1944, pp. 117–124; see also Adams 2021).

The opposition Simpson expressed to orthogenesis in 1941 centered on what he saw as its teleological, predetermined outcome, which implied a cause operating at a high level—possibly even a metaphysical one (on the logic of causation in orthogenesis, see Ceccarelli 2018). He countered with the sufficiency of population genetics to explain evolution. Gaining significance via *Tempo and Mode*, his claims took on new dimensions in his 1949 *Meaning of Evolution*, in which the notion of "higher-level individuality" served as an important target. Deriving from the 1948 Terry Lectures in Science and Religion at Yale, which gave him license for a broad philosophical perspective on the "meaning of evolution," this book had at its base an argument for the sufficiency of a materialist, anti-vitalist, non-teleological explanation of the history of life. Indeed, Simpson (1949, pp. 123–124) presented evolution as a field of evidence upon which vitalist, teleological, and materialist views of life could be tested. Materialism won.

Within this frame, Simpson (1949, Chap. 11) targeted orthogenesis for its frequent association with vitalism via an internal driving principle and for overgeneralizing from a small number of apparent directional trends. One particularly accessible version of the view he opposed was that higher taxonomic groups, like individuals, have a natural lifetime—that they "are born, rise to a period of virility, decline, and die" (1949, p. 187). This invited people incorrectly to view the "death" of a taxonomic group—its extinction—as "a fate implanted in the racial tissues as inevitable

[3] Simpson (1944, p. 97) attributed the terms macro- and microevolution to Richard Goldschmidt, but Adams (2021) notes that it can be traced back through Dobzhansky (1937) to Dobzhansky's mentor Iurii Filipchenko in 1927.

old age and death are implanted in the tissues of individuals,"[4] instead of the outcome of myriad interactions between "populations and their environments" (1949, p. 198). This critique of the analogy of higher-level trends with individual lifetimes would reappear in *Major Features* (1953, pp. 214–215) and was retained, as late as 1967, in the expanded second edition of *Meaning of Evolution*.

In the context of general evolutionary theory, the analogy between the lifetime of organismal individuals and higher taxa had to do with the causes of evolutionary trends—a fundamental problem for the paleontologist in seeking to understand and explain the history of life. But when it came to *human* action, as Simpson had already shown in the individuality article and would develop further in 1949, the stakes were still greater.

The last section of *Meaning of Evolution* squarely addressed the meaning of evolution for humans' place in nature and for the human responsibility deriving from that place. Simpson first argued that humans' consciousness and ability to transmit culture across generations rendered human evolution a new, distinctive kind of evolution that set us apart from the rest of nature and required us to develop an ethic appropriate to humans' place of dominance in the world. But how was that ethic to be derived, and what should it look like (Ruse 1999)? Among the various earlier approaches to a naturalistic ethic, Simpson especially attacked the Gerardian position, which he now called "aggregation ethics." This viewed "as ethically good the increased aggregation of organic units into higher levels of organization," in which lower-level units, like cells, are subordinated to "the so-called organic state, considered as having an individuality and life of its own." It was "thoroughly erroneous" (Simpson 1949, pp. 305–306). In this new, ethics-oriented packaging of his stance, Simpson acknowledged that humans were social animals, and that they were indeed shaped by their participation in social groups. But this did not mean that "socialization" and "individualization" stood in conflict; rather, they worked together to shape human action. Nevertheless, individuals have responsibility for their own behavior. They may work for a common, social goal, but cannot offload responsibility to the group.

Simpson proposed what he called the "knowledge ethic"—to increase knowledge is right, and freedom to do so is good. This ethic required individuals to take responsibility for searching for truth (which grounded the good), testing possible solutions against each other, and communicating the truths thus found. If one could not become an expert oneself, "the moral duty of the nonspecialist is to choose the judgments of that authority whose qualifications are greatest in the pertinent field and whose submitted evidence is best" (Simpson 1949, p. 314). Still, individual humans were responsible for their choices and actions. Simpson didn't hide the political connections here. He wrote flat-out: "Authoritarianism is wrong," and "Totalitarianism is wrong" (1949, pp. 320, 321). Democracy, which "is wrong in many of its current aspects," is better than the others because, when done right, it balances individual responsibility with the welfare of the group (1949, pp. 321–323).

Simpson's opposition both to orthogenesis and to the treatment of higher-level groups as individuals, already united in his 1941 paper, persisted as preoccupations in *Meaning of Evolution*. Though the problems of integration and hierarchy were transposed in 1949 into ethical terms, his words show that political commitments first clearly drawn out during the war were still at work. These two targets shared a structural similarity: in ascribing primary causal agency to a level above the individual organism, both theories subordinated and limited agency (and in the case of humans, responsibility) at the lower level. To be sure, each theory presented its own distinct problems. The association of orthogenesis with vitalism or unknown forces, for instance, was anathema to Simpson, a convinced atheist and determinist; his opposition to Gerard's biological integrationism was explicitly triggered by what he saw as its totalitarian political and moral implications. Here we suggest that his insistence on placing causal agency at a lower level provided a rational and consistent scientific position uniting deeply held convictions, and that those convictions in turn provided moral force for his reductionism.

Analyzing Simpson's evolutionary and political-moral concerns between his 1941 article and his later works suggests a trajectory in which he was working out the implications of both, together, over the next dozen years, even when he wrote about them separately. Their mutual reinforcement may provide at least a partial explanation for some of the differences between *Tempo and Mode* (1944) and its successor, *Major Features of Evolution* (1953). As Gould (2002, pp. 528–531) has argued, a major difference between the two was that, whereas in 1944, Simpson's "quantum evolution" represented something different in kind from "phyletic" evolution (in which the tempo and mode of evolutionary change are more or less uniform and gradual), by 1953, it was different only in degree, and adaptation played a significantly more prominent role. This contributed to what Gould called the "hardening of the Synthesis," its rejection of nonadaptive processes in evolution and of macroevolution as having anything beyond trivial significance. Between these two books, among many other events, were Simpson's forays into a more serious consideration of the philosophy of science and evolutionary ethics—foreshadowed by his 1941 article

[4] Simpson used the term "racial" here as a general term covering all higher taxa, not for "races" as varieties within a species. In 1949, the term "taxon" was only just beginning to be used more broadly, and Simpson did not use it.

and worked out more fully in *Meaning of Evolution*. When we put these together, we have a more cogent picture of how lower-level causes might have risen in his estimation—not through an entirely rational process, but through the juxtaposition of two emotionally powerful concerns that were both resolved through setting the action at the level of properly "individual" agency.

Despite these commitments, already in the 1950s Simpson's views on the evolutionary centrality of the individual organism grew more flexible, as he increasingly emphasized the critical evolutionary significance of the population (Grodwohl 2019). As he put it (1958, p. 14), "The medium of evolution, the thing in which the processes of evolution occur and hence the thing that is actually evolving, is a population." Extending this thought, but without endorsing any notion of group selection, he elaborated (p. 20):

> Now it is evident that selection favors successful reproduction of the population and not necessarily of any or of all particular individuals within it. A striking, although rather exceptional, example of that fact is provided by the social insects, among which only a very small fraction actually reproduce although their success in reproduction is completely dependent on the nonreproducing individuals.

It seems significant here that, as the Modern Synthesis was still gaining adherents, and consistent with his continued opposition to organicism, Simpson avoided representing populations as an individual-like entity (despite its being a "thing") and represented social insects as populations rather than as superorganisms.

And what of the biological concepts and the scientists that Simpson was criticizing? The generally accepted narrative of the Chicago Ecologists follows "a shift among ecologists from 'good of the species' arguments to individual selectionist accounts of adaptations" in the 1950s (Mitman 1992, p. 122; see also Wilson 1983; Keulartz 1998). Hierarchical notions of multiple levels of individuals all functioning as parts of correspondingly functioning wholes, the importance of adaptation and selection at the level of the group, both tied to cooperation and increasing integration for the welfare of both the parts and the whole, were already under attack by Simpson. They withered further in scientific prominence following George C. Williams' *Adaptation and Natural Selection* (1966), its reductionist gene's eye view of adaptive evolution and its denial that group adaptation exists (Sober and Wilson 2011; Boomsma 2016). This general view would not be seriously challenged by evolutionary theorists until the 1980s (e.g., Wilson 1983; Damuth and Heisler 1988).

Yet despite this prevalent narrative, an undercurrent of ideas from the early work of the Chicago Ecologists and close associates like Emerson and Gerard continued to flow and transform not far below the surface of the broader scientific enterprise. With added impetus from the likes of Ludwig von Bertalanffy, ideas of organismic integration and hierarchy would resurface later in revised and influential forms—perhaps most prominently when Gerard joined with Kenneth Boulding and Anatol Rapaport in the early 1950s to found General Systems Theory (Hammond 2003). While Gerard did not play a direct role instituting systems ecology, a major research area in the 1950s and 1960s, some of his organicist principles were adopted by leading systems ecologists, including Eugene and Howard Odum (Hammond 2003; Voigt 2011). Today systems thinking is dispersed across biology and many other domains of science (Assche et al. 2019; Hammond 2019).

Another facet of Emerson and Gerard's organicist views, cooperation and organismality, has had a similarly up-and-down history. Emerson's concept of the superorganism, itself built on a foundation laid earlier by William Morton Wheeler (1911), flourished for a time, but then faded in the late 1960s in the face of the increasing genetic reductionism of the era (Gibson et al. 2012). More recently, however, it has resurfaced in the work of researchers on social evolution among animal colonies, prokaryotes, microbes, and various symbiont relationships (e.g., Queller and Strassmann 2009). In tracing the historical "roots" of multilevel selection, Gibson et al. (2012, p. 505) show how Emerson "artfully united the multilevel theory of 'emergent evolution' with natural selection in a way that differs but little from the theory of multilevel selection that many scientists and scholars now promote." Even more significantly, the superorganism concept, in much-revised and genetically-aware form, has returned to prominence in studies of complex eusociality (Haber 2013; Boomsma and Gawne 2018; Canciani et al. 2019). We will refrain from the arduous effort needed to trace how these developments are intertwined with the complicated, politically inflected history of scientific debates over group selection and sociobiology (Caplan 1978; Segerstråle 2000), only noting that here, too, the early influence of Emerson and Gerard is present (Shavit 2004; Gibson 2013; Canciani et al. 2019). In fact, different interpretations of groups and different kinds of group fitness have been used in the evolutionary biology literature in different ways (Shavit 2004; Okasha 2006; Wilson 2007; Leigh 2010). The consensus view, if there even is one, has become both more nuanced and more multifaceted as time goes on.

Conclusion

In 1988, Evelyn Fox Keller wrote on evolutionary discourse:

> [W]hatever the choice of unit of selection, wherever the individual is located in evolutionary biology, that individual serves this discourse as a demarcator

> between two sets of values. In the first set, we have autonomy, competition, simplicity; a theoretical privileging of chance and random interactions, and the interchangeability (i.e., equality) of units. In the second set, we have interdependence, cooperation, complexity; the theoretical privileging of purposive and functional dynamics, and often a hierarchical organization. (1988, p. 195)

Keller went on to call the first set "public" values—ones that reflected multiple individuals interacting with one another—and the second set "private," focused on interiority. Though not discussed particularly as an example in Keller's article, Simpson's differences with the Chicago Ecologists perfectly fit the dichotomy she draws. Indeed, Gregg Mitman (1992) and Ayelit Shavit (2004) have shown how closely the political values and ideologies of the evolutionary synthesists and the Chicago Ecologists map onto this dichotomy. What Keller called individuality's "public" values meshed well with the American version of democracy propounded by Simpson and others in the 1940s and 1950s, whereas the Chicago Ecologists' association with a more cooperationist ideal was readily tarred with a totalitarian brush in that period. As Mitman has summarized, for many American Cold War intellectuals, "Difference, diversity, and conflict were the preserving forces of a democratic society; cooperation and group solidarity were not" (1992, p. 205; see also Turner 2013).

We argued in a recent essay that when the concept "individuality" is put to work, its applied meanings are contextual, contingent upon different perspectives and disciplinary problems (Lidgard and Nyhart 2017b; see also Kaiser and Trappes 2021). Simpson's paper, and the analysis of the broader historical setting its content demands, invite us to recognize that the relevant contexts are not just scientific. The situations in which different logics of individuality were developed and applied made a difference. Gerard's desire to create an all-encompassing theory of hierarchical integration, inclusive of humans, led him to treat totalitarianism as an anomalous distortion that would be short-lived (1940c). Simpson's commitment to the evolutionary agency of individual organisms, already reinforced by his abhorrence of Osborne's "metaphysical" orthogenesis, was intensified via his public engagement with politics and ethics. Does this mean that either Gerard's or Simpson's science was bad science? No. It was science made by humans, initially in a time of political crisis, in settings in which political considerations were understood to be relevant. As relevant contexts change, different features will be perceived as apposite to the problems scientists are trying to solve, and different language, different metaphors and analogies will come to seem appropriate to explore (Reynolds 2018). As we hope to have shown in this introduction, that sort of exploration—exploration of as yet unidentified contexts, among both biologists and historians—deserves greater appreciation.

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References

Adams MB (2021) Little evolution, BIG evolution: rethinking the history of Darwinism, population genetics, and the "Synthesis." In: Delisle RG (ed) Natural selection revisiting its explanatory role in evolutionary biology. Springer, Cham, pp 195–229. https://doi.org/10.1007/978-3-030-65536-5_8

Allee WC, Emerson AE, Park O, Park T, Schmidt KP (1949) Principles of animal ecology. Saunders, Philadelphia

Assche KV, Valentinov V, Verschraegen G (2019) Ludwig von Bertalanffy and his enduring relevance: celebrating 50 years general system theory. Syst Res Behav Sci 36:251–254. https://doi.org/10.1002/sres.2589

Baedke J (2019) What is a biological individual? In: Martín-Durán JM, Vellutini BC (eds) Old questions and young approaches to animal evolution. Springer, Cham, pp 269–284

Boomsma JJ (2016) Fifty years of illumination about the natural levels of adaptation. Curr Biol 26:R1250–R1255. https://doi.org/10.1016/j.cub.2016.11.034

Boomsma JJ, Gawne R (2018) Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation. Biol Rev 93:28–54. https://doi.org/10.1111/brv.12330

Bouchard F, Huneman P (eds) (2013) From groups to individuals: evolution and emerging individuality. MIT Press, Cambridge

Cain J (2009) Ritual patricide: why Stephen Jay Gould assassinated George Gaylord Simpson. In: Sepkoski D, Ruse M (eds) The paleobiological revolution: essays on the growth of modern paleontology. University of Chicago Press, Chicago, pp 346–363

Canciani M, Arnellos A, Moreno A (2019) Revising the superorganism: an organizational approach to complex eusociality. Front Psychol 10:1–12. https://doi.org/10.3389/fpsyg.2019.02653

Caplan AL (ed) (1978) The sociobiology debate: readings on ethical and scientific issues. Harper & Row, New York

Ceccarelli D (2018) Orthogenetic predictability: orderliness and symmetry in early macroevolutionary explanations. In: Ceccarelli D, Frezza G (eds) Predictability and the unpredictable: life, evolution and behavior. CNR Edizioni, Rome, pp 177–192

Ceccarelli D (2021) Recasting natural selection: Osborn and the pluralistic view of life. In: Delisle RG (ed) Natural selection: revisiting its explanatory role in evolutionary biology. Springer, Cham, pp 171–191. https://doi.org/10.1007/978-3-030-65536-5_7

Child CM (1915) Individuality in organisms. University of Chicago Press, Chicago

Damuth J, Heisler IL (1988) Alternative formulations of multilevel selection. Biol Philos 3:407–430. https://doi.org/10.1007/BF00647962

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Dobzhansky T (1937) Genetics and the origin of species. Columbia University Press, New York

Emerson AE (1939) Social coordination and the superorganism. Am Midl Nat 21:182–209

Emerson AE (1946) The biological basis of social cooperation. Ill Acad Sci Trans 39:9–18

Esposito M (2017) The organismal synthesis: holistic science and developmental evolution in the English-speaking world, 1915–1954. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 219–241. https://doi.org/10.1007/978-3-319-69123-7_10
Fitch WM, Ayala FJ (eds) (1995) Tempo and mode in evolution: genetics and paleontology 50 years after Simpson. National Academy Press, Washington, DC
Gerard RW (1940a) Organism, society and science. I. Sci Mon 50:340–350
Gerard RW (1940b) Organism, society and science. II. Sci Mon 50:403–412
Gerard RW (1940c) Organic freedom. In: Anshen RN (ed) Freedom: its meaning. Harcourt, Brace, New York, pp 412–427
Gerard RW (1942) Higher levels of integration. Science 95:309–313
Gerard RW (1957) Units and concepts of biology. Science 125:429–433
Gerard RW (1958) Concepts and principles of biology. Behav Sci 3:95–102
Gibson AH (2013) Edward O. Wilson and the organicist tradition. J Hist Biol 46:599–630. https://doi.org/10.1007/s10739-012-9347-3
Gibson AH, Kwapich CL, Lang M (2012) The roots of multilevel selection: concepts of biological individuality in the early twentieth century. Hist Philos Life Sci 35:505–532. https://doi.org/10.1007/978-3-319-78677-3_2
Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge
Grodwohl J-B (2019) Animal behavior, population biology and the Modern Synthesis (1955–1985). J Hist Biol 52:597–633. https://doi.org/10.1007/s10739-018-9553-8
Haber M (2013) Colonies are individuals: revisiting the superorganism revival. In: Bouchard F, Huneman P (eds) From groups to individuals: evolution and emerging individuality. MIT Press, Cambridge, pp 195–216. https://doi.org/10.7551/mitpress/8921.003.0015
Hagen J (2003) The statistical frame of mind in systematic biology from quantitative zoology to biometry. J Hist Biol 36:353–384. https://doi.org/10.1023/A:1024479322226
Hammond D (2003) The science of synthesis: exploring the social implications of general systems theory. University Press of Colorado, Boulder
Hammond D (2019) The legacy of Ludwig von Bertalanffy and its relevance for our time. Syst Res Behav Sci 36:301–307. https://doi.org/10.1002/sres.2598
Hollinger DA (1996) The defense of democracy and Robert K. Merton's formulation of the scientific ethos. In: Hollinger D (ed) Science, Jews, and secular culture: studies in mid-twentieth century American intellectual history. Princeton University Press, Princeton, pp 80–96
Hopkins MJ, Lidgard S (2012) Evolutionary mode routinely varies among morphological traits within fossil species lineages. Proc Natl Acad Sci USA 109:20520–20525. https://doi.org/10.1073/pnas.1209901109
Jarvis JU (1981) Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. Science 212:571–573
Kaiser MI, Trappes R (2021) Broadening the problem agenda of biological individuality: individual differences, uniqueness and temporality. Biol Philos 36:1–28. https://doi.org/10.1007/s10539-021-09791-5
Keller EF (1988) Demarcating public from private values in evolutionary discourse. J Hist Biol 21:195–211. https://doi.org/10.1007/BF00146986
Keulartz J (1998) The struggle for nature: a critique of radical ecology. Routledge, New York
Laporte LF (2000) George Gaylord Simpson: paleontologist and evolutionist. Columbia University Press, New York
Leigh EG Jr (2010) The group selection controversy. J Evol Biol 23:6–19. https://doi.org/10.1111/j.1420-9101.2009.01876.x
Lidgard S, Nyhart LK (2017a) Biological individuality: integrating scientific, philosophical, and historical perspectives. University of Chicago Press, Chicago
Lidgard S, Nyhart LK (2017b) The work of biological individuality: concepts and contexts. In: Lidgard S, Nyhart LK (eds) Biological individuality: integrating scientific, philosophical, and historical perspectives. University of Chicago Press, Chicago, pp 17–52
Liow LH (2004) A test of Simpson's "rule of the survival of the relatively unspecialized" using fossil crinoids. Am Nat 164:431–443. https://doi.org/10.1086/423673
Mitman G (1992) The state of nature: ecology, community, and American social thought, 1900–1950. University of Chicago Press, Chicago
Nicholson DJ, Gawne R (2015) Neither logical empiricism nor vitalism, but organicism: what the philosophy of biology was. Hist Philos Life Sci 37:345–381. https://doi.org/10.1007/s40656-015-0085-7
Okasha S (2006) Evolution and the levels of selection. Oxford University Press, Oxford
Olson EC (1991) George Gaylord Simpson 1902–1984: a biographical memoir. National Academy of Sciences USA, Washington, D.C.
Osborn HF (1931) The nine principles of evolution revealed by paleontology. Am Nat 66:52–60
Osborn HF (1934) Aristogenesis, the creative principle in the origin of species. Am Nat 68:193–235. https://doi.org/10.1086/280541
Queller DC, Strassmann JE (2009) Beyond society: the evolution of organismality. Philos Trans R Soc Lond B Biol Sci 364:3143–3155. https://doi.org/10.1098/rstb.2009.0095
Reynolds AS (2018) The third lens: metaphor and the creation of modern cell biology. University of Chicago Press, Chicago
Ruse M (1999) Evolutionary ethics in the twentieth century: Julian Sorell Huxley and George Gaylord Simpson. In: Maienschein J, Ruse M (eds) Biology and the foundations of ethics. Cambridge University Press, New York, pp 198–224
Segerstråle U (2000) Defenders of the truth: the battle for science in the sociobiology debate and beyond. Oxford University Press, New York
Sepkoski D (2019) The unfinished synthesis? Paleontology and evolutionary biology in the 20th century. J Hist Biol 52:687–703. https://doi.org/10.1007/s10739-018-9537-8
Shavit A (2004) Shifting values partly explain the debate over group selection. Stud Hist Philos Sci C Stud Hist Philos Biol Biomed Sci 35:697–720. https://doi.org/10.1016/j.shpsc.2004.09.007
Simpson GG (1937) Patterns of phyletic evolution. GSA Bull 48:303–314
Simpson GG (1941) The role of the individual in evolution. J Wash Acad Sci 31:1–20
Simpson GG (1944) Tempo and mode in evolution. Columbia University Press, New York
Simpson GG (1949) The meaning of evolution: a study of the history of life and of its significance for man. Yale University Press, New Haven
Simpson GG (1953) The major features of evolution. Columbia University Press, New York
Simpson GG (1958) The study of evolution: methods and present status of theory. In: Roe A, Simpson GG (eds) Behavior and evolution. Yale University Press, New Haven, pp 7–26
Simpson GG (1964) This view of life: the world of an evolutionist. Harcourt, Brace & World, New York
Simpson GG (1966) Naturalistic ethics and the social sciences. Am Psychol 21:27–36. https://doi.org/10.1037/h0021106
Simpson GG (1967) The meaning of evolution, revised edn. Yale University Press, New Haven
Simpson GG (1969) Biology and man. Harcourt Brace & World, New York

Simpson GG, Roe A (1939) Quantitative zoology: numerical concepts and methods in the study of recent and fossil animals. McGraw-Hill, New York

Smocovitis VB (2016) The unifying vision: Julian Huxley, evolutionary humanism and the evolutionary synthesis. In: Kamminga H, Somsen G (eds) Pursuing the unity of science: ideology and scientific practice from the Great War to the Cold War. Routledge, London, pp 30–49

Sober E, Wilson DS (2011) Adaptation and natural selection revisited. J Evol Biol 24:462–468. https://doi.org/10.1111/j.1420-9101.2010.02162.x

Turner F (2013) The democratic surround: multimedia and American liberalism from World War II to the psychedelic sixties. University of Chicago Press, Chicago

Voigt A (2011) The rise of systems theory in ecology. In: Schwarz A, Jax K (eds) Ecology revisited: reflecting on concepts, advancing science. Springer, Dordrecht, pp 183–194. https://doi.org/10.1007/978-90-481-9744-6_15

Wheeler WM (1911) The ant-colony as an organism. J Morphol 22:307–325

Whitman W (1940) Leaves of grass. Doubleday, Doran, New York

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Wilson DS (1983) The group selection controversy: history and current status. Annu Rev Ecol Syst 14:159–187. https://doi.org/10.1146/annurev.es.14.110183.001111

Wilson RA (2007) Levels of selection. In: Matthen M, Stephens C (eds) Handbook of the philosophy of science. Philosophy of biology. Elsevier, Amsterdam, pp 141–162

Winther RG (2005) An obstacle to unification in biological social science. Formal and compositional styles of science. Grad J Soc Sci 2:40–100

Wolfe AJ (2018) Freedom's laboratory: the Cold War struggle for the soul of science. Johns Hopkins, Baltimore