Hist. Phil. Life Sci., 35 (2013), 505-532

# The Roots of Multilevel Selection: Concepts of Biological Individuality in the Early Twentieth Century

Abraham H. Gibson
*Department of History, Florida State University*
*401 Bellamy Building, 113 Collegiate Loop, Tallahassee, FL 32306, USA*
*ahgibson@fsu.edu*

Christina L. Kwapich
*Department of Biological Sciences, Florida State University*
*319 Stadium Drive, Tallahassee, FL 32306, USA*
*ckwapich@bio.fsu.edu*

Martha Lang
*Department of Philosophy, Florida State University*
*151 Dodd Hall, Tallahassee, FL 32306, USA*
*mll@fsu.edu*

ABSTRACT - As multilevel selection theory has gained greater acceptance over the past quarter-century, scientists and scholars have shown an increased interest in the theory's historical antecedents. Despite this interest, however, the early twentieth century remains largely unexplored. It is generally assumed that biologists thought "naïvely" about evolutionary dynamics during this era, and that their attempts to explain biological phenomena often lacked sophistication. Now that several recent works have called attention to the complex relationship between biological individuality and the levels of selection, we believe it will prove instructive to revisit these early-twentieth-century biologists and reassess their criteria for biological individuality. Doing so reveals that they constructed a multilevel explanation of evolution that anticipated modern interpretations in several important ways. Though it is certainly true that most of these early biologists failed to recognize natural selection's pervasive agency, it is no less true that one of them, termite expert Alfred 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. After reviewing the historical record, we place these early-twentieth-century biologists in their proper historical context, and we compare their interpretation of evolution with modern interpretations.

KEYWORDS - Multilevel selection, biological individuality, emergent evolution

*A collection of individual notes does not in itself form a melody; the melody comes only when we produce a particular arrangement of the individual notes. Harmony, therefore, is produced by the mental activity which recognizes the proportional relationships between the multiplicity of individual parts.*

Johannes Kepler, 1619 (Emerson 1939, 182)

For several decades following the end of World War II, biologists generally agreed that natural selection targets individual organisms, or the genes of which they are comprised, and that apparent selection at higher levels was illusory. Over the past twenty-five years, however, an increasing number of scientists and philosophers of biology have challenged this assumption from diverse discipline-specific perspectives. Many now promote multilevel selection, which, generally speaking, regards individuals and groups as context dependent. In other words, that which is an individual in one context might be a group in another, and vice versa. According to this interpretation, life on earth is comprised of a hierarchy of individuals (genes, organelles, cells, metazoans, populations, communities, etc.), each one contained within the next, all of them governed by natural selection. The theory, while not wholly uncontroversial, is now being used to explain many of biology's most vexing mysteries, including the nature of individuality, the major transitions in evolutionary history, and the theoretical foundations of sociobiology.[1] Disparate topics that were previously examined in isolation from one another (including the origin of life, endosymbiosis, the first multicellular organisms, insect eusociality, and the ecological relationships within multi-species communities) are now being folded into an elegant evolutionary framework that engages a variety of disciplines and encompasses every level of the biological hierarchy, from microscopic proteins to macroscopic communities.[2]

As interest in multilevel selection has grown, many scientists and

[1] Much of the controversy stems from philosophical debates surrounding the embedded concepts of emergence, reductionism, and downward causation. See Kim (1999) and Rosenberg (2006).

[2] Representative works from both the sciences and the humanities include, but are not limited to, the following: Arnold and Fristrup (1982), Wade (1982), Buss (1987), Szathmáry and Demeter (1987), Damuth and Heisler (1988), Lloyd (1988), D.S. Wilson and Sober (1989), Brandon (1990), Sapp (1994), D.S. Wilson and Sober (1994), Sober and D. S. Wilson (1997), Maynard Smith and Szathmáry (1995), Michod (1997), D.S. Wilson (1997a), Michod (1999), Goodnight and Wade (2000), D.S. Wilson (2001), Korb and Heinze (2004), Okasha (2005), Okasha (2006), Elwick (2007), D.S. Wilson and E.O. Wilson (2007), Arp (2008), O'Fallon (2008), Martens (2010), Folse and Roughgarden (2010), Sapp (2010), Wade et al. (2010), Harman (2010), Bouchard (2010), Calcott et al. (2011), Nyhart (2011), D.S. Wilson (2011), Gilbert et al. (2012), Clarke (2012), Corning (2012), Goldsby (2012), Denton et al. (2013).

scholars have sought to recover the theory's historical antecedents, and they have generated extraordinarily valuable scholarship in the process. In their respective works, for example, James Elwick, Lynn Nyhart and Scott Lidgard have all shown that biologists were deeply interested in questions about individuality at different levels in the decades preceding the publication of *On the Origin of Species* (Elwick 2007; Nyhart and Lidgard 2011). Perhaps not surprisingly, many scholars have also attempted to parse Darwin's thoughts on the matter, though it should be noted that all the attention has so far failed to determine whether Darwin believed in individual selection solely (Ruse 1980; Dugatkin 1997; Gardner et al. 2011), or whether he also allowed for selection at other levels (Borrello 2005; Eldakar and D.S. Wilson 2011). Finally, scholars have also spent a significant amount of time analyzing the "traditional levels-of-selection discussions of the 1960s and 1970s" (Okasha 2005, 1013), when biologists like George C. Williams (1966), William Hamilton (1964a; 1964b), Edward O. Wilson (1975), and Richard Dawkins (1976) purportedly dismantled multilevel interpretations of the sort put forth by V.C. Wynne Edwards (1962) once and for all. These scientists dismissed the idea that individuals had traits that promoted the survival of their population or species, and instead endorsed the idea that the persistence of species and populations arises from the differential reproduction of individuals.

And yet, despite this interest in the historical origins of multilevel selection theory, there remains at least one large gap in the historiography: the early twentieth century. Nyhart and Lidgard provide an excellent history of individuality research in the nineteenth century, but their temporal focus affords the first half of the twentieth century just two paragraphs. More often, biologists from the early twentieth century are acknowledged but then summarily dismissed. It is generally assumed that biologists "thought naively about group selection" during the early twentieth century, thereby preventing the articulation of a more formal theory of multilevel selection (D.S. Wilson and E.O. Wilson 2008, 381). Biologist David Sloan Wilson, whose name is synonymous with the levels-of-selection debate, has remarked that "multilevel selection did not emerge as a major issue until the 1960s" (D.S. Wilson 1997b, s2). In a similar fashion, historian Mark Borrello (2010) provides an excellent history of group selection, though he too trains most of his focus on the second half of the twentieth century.

Despite the widely held belief that biologists "thought naively" about such matters during the early twentieth century, there is evidence to suggest they were slowly groping toward a multilevel interpretation of evolution that was, in several important ways, similar to the generalized multilevel theories advocated in academic circles today. To demonstrate as much, we will examine three otherwise distinct fields of biology (sponge biology, entomology, and plant ecology) between 1900 and 1939. Although practitioners in these fields addressed organisms that were not only far removed from one another in a phylogenetic sense, but also located at different levels of the biological hierarchy, they nevertheless discerned strikingly similar phenomena. In each field, biologists observed collections of otherwise autonomous individuals integrating with one another to produce individuals of a higher order still. What is more, they developed similar explanations for the mysterious organizational impulse that suffused these cooperative individuals. Some clearly believed that they were all studying the same fundamental principle, manifest at different levels.

Their efforts culminated during the interwar respite (1919-1939), when they converged on a bold, new interpretation of the universe known as *emergent evolution*. First named and articulated by C. Lloyd Morgan (1923), the theory sought to explain the appearance of entirely new properties at certain critical stages in the course of evolution. It was one of many organicist philosophies that proved popular during the interwar period (Henderson 1917; Spaulding 1918; Alexander 1920; Sellars 1922; Parker 1924; Broad 1925; Whitehead 1925; Smuts 1926), but, as its name suggests, emergent evolution was the only one that placed emergence at the heart of a philosophy of evolution (Blitz 1992, 2). As a result, the theory achieved widespread popularity among evolutionary biologists (an anachronistic label, but no less accurate) who sought an explanation for the slippery nature of biological individuality.[3] Contrary to Darwinian dogma, these biologists insisted that cooperation had influenced the course of evolution just as much as competition, and that this tendency toward cohesion sometimes resulted in new individuals at multiple levels of the biological hierarchy.

Other scientists and scholars have explored particular aspects of this wide-ranging history, but they seldom compare phenomena located at different levels of the biological hierarchy.[4] We have no interest in overselling the modernity of these early biologists, most of whom failed to appreciate natural selection's pervasive agency and underestimated what later became known as the free-rider problem. Nevertheless, we also

[3] According to Google Ngram, the phrase "evolutionary biology" did not gain widespread currency until the 1970s. See also: E.O. Wilson (1994, 227).

[4] See, for example: Worster (1977), Simberloff (1980), Tobey (1981), Todes (1989), D.S. Wilson and Sober (1989), Blitz (1992), McCoy and Schrader-Frechette (1992), Mitchell (1995), Mitman (1992), J. Wilson (1999), Keller and Golley (2000), Anker (2001), Kohler (2002), Corning (2005), Clayton and Davies (2006), Dugatkin (2006), Sleigh (2007), Hölldobler and E.O. Wilson (2008), Borrello (2010), Corning (2012).

think that their contributions have been misrepresented for too long. Examining concepts of biological individuality during the early twentieth century allows one to not only retrace the historical origins of multilevel selection, but also allows one to revisit an era regarded by many historians of biology as the eclipse of Darwinism (Bowler 1983). It was a time, so the story goes, when biologists abandoned natural selection in favor of alternative mechanisms. On these grounds, contemporary scholars often dismiss their contributions to evolutionary thought. And yet, as historian Mark Largent explains, "the era of the so-called eclipse of Darwinism was, in fact, a dynamic and exciting time in the history of evolutionary biology" (Largent 2009, 16). Indeed, it was a time when biologists from a variety of fields developed a multilevel interpretation of evolution that supported Darwinism in some ways, and challenged it in others.

## The sponge and its multilevel individuality

Few creatures have inspired more debate among biologists than the enigmatic sponge. Though naturalists have studied the sponge since antiquity (Voultsiadou 2007), they have seldom agreed on its most basic properties, and did not conclusively establish the creature's animality until the late eighteenth century (Levi 1999). That dispute had scarcely been settled when another began to take shape. "It is difficult to determine whether sponges are single or compound individuals," America's foremost microscopist, Henry James-Clark, reported in 1865 (James-Clark 1865, 40). Accordingly, he sometimes referred to the monads in a sponge as "individual members of a colony" (James-Clark 1866, 324), though he elsewhere refined his position, stating that each monad was but a single head on a "polycephalic individual" (James-Clark 1871, 426). By the turn of the century, Edward A. Minchin, professor of zoology at University College London, had likewise weighed in on the individuality of a sponge. He insisted that "a sponge consists of as many persons as there are oscular openings." Because the sponge requires a functioning osculum (vent) in order to feed and grow, he concluded that the osculum represents a "physiological, as well as morphological, center, and thus presents from several points of view the most satisfactory criterion of sponge individuality" (Minchin 1900, 91).

Henry Van Peters Wilson, professor of biology at the University of North Carolina, turned the debate on its head in 1907, when he published the results of a fascinating, if somewhat crude, experiment. Wilson cut and crumbled a sponge (*Microciona*) into tiny pieces and forced the fragments through a fine metal sieve. Doing so wrenched apart the sponge's constituent cells, so that each was physically distinct from the others for the first time in its history. Torn utterly asunder, the dissociated sponge cells were thrown into a bucket of saltwater. When the cells finally settled along the bottom, something remarkable happened. "Fusion of the granular cells begins immediately," Wilson wrote, "and in a few minutes time most of them have united to form small conglomerate masses." Within a few days, the reunited cells had differentiated with dermal cells along the exterior and flagellated chambers along the interior, thereby reconstituting a fully functioning sponge. Though Wilson generally refrained from philosophical musings, the experiment's implications were not lost on him. "To such a mass, the ordinary idea of the individual is not applicable," he drily observed (Wilson 1907, 164-166).

Not surprisingly, Wilson's paper caught the attention of naturalists both in the United States and abroad. Among the first to explore the experiment's implications for biological individuality was a recent Oxford grad named Julian Huxley. In 1909, twenty-year-old Huxley accepted a fellowship at Anton Dohrn's famed Zoological Station in Naples, where he repeated Wilson's experiment using the *Sycon* sponge. Following Wilson's lead, Huxley crushed the sponge into tiny pieces and forced its mushy fragments through a fine mesh. Observing through a microscope, Huxley confirmed that the cells not only survived their violent severance from one another, but were "scarcely inconvenienced" by the new arrangement. This impressive autonomy convinced him that the cells in a sponge showcase all the hallmarks of true individuality. "Though the whole sponge is a true individual, composed of harmonious parts," he wrote, "yet those parts can themselves behave as harmonious wholes" (Huxley 1912, 92-98).

Nor was that the experiment's only revelation. Again following Wilson's lead, Huxley described how the dissociated cells moved across the bottom of the tank in amoeboid fashion, as if searching for one another. Joining up to form an undifferentiated globule, the collar cells and dermal cells soon began to sort themselves out. Over the course of several days, this random collection of cells became "an actual sponge, living and functioning, similar in every way to one that has grown up from the egg." As such, Huxley concluded that the cells were also obviously subject to a higher individuality. "There seems to be a strange organizing power superior in kind to the powers of the cells themselves – an idea of the whole informing the parts," he observed. Huxley felt that this kind of single-minded coordination conjured the image of a general directing his army, or an architect arranging his materials, but alas there was none. "Where is the general, where the architect?" he rhetorically asked. Though he feigned no hypothesis regarding the force that compelled these cells to unite, calling it "one of the most mysterious problems of life," he suspected the explanation was somehow latent in the evolutionary process (Huxley 1912, 116).

To prove as much, Huxley modified Wilson's famous experiment by isolating the dissociated collar cells from the rest of the sponge material. Remarkably, rather than reconstitute a sponge, these specialized cells formed a spherical mass identical in nature to a "colony of choanoflagellates." Though he cautioned against inferring too much, Huxley ultimately interpreted his results as evidence that sponges are descended from "cells which existed as free-living and independent individuals." Over the course of countless generations, these cells ceded more and more of their individuality to the colony, thereby enabling multicellularity. "Each [cell] preserves a considerable measure of independence," Huxley observed, "and is yet subordinated to the good of the whole. This resulted in the metazoan type of structure, where the individual is built up out of a number of cells instead of one." Significantly, Huxley recognized the exact same process at other levels of the biological hierarchy. "So it comes to pass," he wrote, "that the continuous change which is passing through the organic world appears as a succession of phases of equilibrium, each one on a higher average plane of independence than the one before, and each inevitably calling up and giving place to one still higher" (Huxley 1912, 92, 116).

Although "emergence" was not part of the scientific lexicon when Huxley published the results of his experiments in 1912, the process that he described was strikingly similar to it. The "whole is greater than the sum of its parts," he explained, "for the problem is one of combination, not of mere addition" (Huxley 1912, 92). Not surprisingly, when Lloyd Morgan's term "emergent evolution" came into vogue in the early 1920s, Huxley was among its earliest acolytes. Reviewing the aforementioned evidence for the origin of multicellularity, Huxley concluded that "there is therefore no possibility of denying that individuality may be acquired by, or imposed upon, what was originally a mere aggregate" (Huxley 1926, 307). What is more, he clearly recognized that this would require between-group dynamics. "Once cooperation exists," Huxley wrote, "competition between the cooperative units is necessary to bring out the full efficiency of their combination" (Huxley 1923, 97). Finally, and perhaps most significantly, he recognized that this view of evolution rendered the notion of an individual context-dependent. "Individuality is always a relative conception," he wrote, adding that "one and the same object may be under one aspect an individual, under another a constituent part of a larger individuality." Because this principle applied equally well throughout the biological hierarchy, he concluded that "there are all levels of individuality" (Huxley 1926, 318). These remarkable conclusions should not be taken lightly. Scientists and scholars have only recently begun to probe the connections between biological individuality and the levels of selection, yet Huxley had already started down the same path more than eighty years ago. Though he never explicitly credited natural selection with demarcating and maintaining individuals at different levels during this era, his interpretation cannot be considered hopelessly "naïve" either.

## Social insect colonies as true individuals

Though naturalists have studied social insects for thousands of years, they did not explicitly compare the colony to an organism until the late nineteenth century. Among the first to do so was Herbert Spencer, the most widely read philosopher in the United States during that time and a polymath by any measure. His interest in human sociality naturally led him to the social insects, which he deemed the most instructive examples of nonhuman "super-organic" phenomena. Citing the insect colony's self-organized division of labor, Spencer observed that "the growths and developments of these social aggregates have analogies with the growths and developments of the individual aggregates." What is more, Spencer alluded to the distinction between germ and soma when he wrote that, "just as the germ of a wasp evolves into a complete individual; so does the adult queen-wasp, the germ of a wasp-society, evolve into a multitude of individuals with definitely-adjusted arrangements and activities" (Spencer 1881, 5). Indeed, though Spencer and Weismann famously disagreed on the prime mechanism of evolution (Osborn 1894), they both agreed that the insect colony, comprised though it was of multiple individuals, itself resembled an individual organism. "The whole colony behaves as a single animal; the state is selected, not the single individual; and the various forms behave exactly like the parts of one individual in the course of ordinary selection," Weismann wrote (1893, 326).

There was probably no biologist more actively engaged in multilevel research during the early twentieth century than Harvard myrmecologist William Morton Wheeler. During a now-famous address at the Woods Hole Marine Laboratory in 1910, Wheeler insisted that the similarities between a multicellular organism and an ant colony were more than incidental. He reminded his colleagues that the ant colony was reproductively differentiated, and thus adhered to Weismann's concept of the organism. He also drew comparisons between the lifespan of a colony and the ontogenetic development of an individual organism. Despite these functional similarities, however, Wheeler explicitly stated that "the most general organismal character of the ant-colony is its individuality" (Wheeler 1911, 131).

Wheeler was interested in more than just ants. He also cited developments in other fields as evidence that individuals could manifest at every level of the biological hierarchy, from the subcellular to the ecological. "If the cell is a colony of lower physiological units, or biophores, as some cytologists believe, we must face the fact that all organisms are colonial or social and that one of the fundamental tendencies of life is sociogenic," he wrote. In his opinion, this coordinating impulse had produced true individuals at every level of the biological hierarchy, from the cellular to the multicellular, from the colonial to the biocoenoses. "Every organism manifests a strong predilection for seeking out other organisms and either assimilating them or cooperating with them to form a more comprehensive and efficient individual" (Wheeler 1911, 142).

Wheeler's interest in the various "levels" of evolution reflected his "obsession with hierarchies and the related phenomenon of emergence" (Sleigh 2004, 160). Despite his enthusiasm, however, he worried that words failed to capture the concept's dynamism. "These sections have been called levels," he wrote. "The word is not very apt since it conveys a spatial and static metaphor, whereas emergents must be regarded as intensively manifold spaciotemporal events" (Wheeler 1928, 22). He eventually became the nation's foremost advocate for emergent evolution during the late 1920s, publishing several books and articles on the topic. Though he opted for Lloyd Morgan's terminology, Wheeler freely acknowledged that others (including Roy Sellars [1922], Jan Smuts [1926], Samuel Alexander [1920], and George Howard Parker [1924]) had applied different labels, including *organicism* and *holism*, to the exact same process (Wheeler 1926, 433).

Wheeler cited the process known as trophallaxis, the reciprocal sharing of liquid foodstuffs through direct, oral transfer, as the "source of the social habit" in social insects (Wheeler 1918), but he never offered a convincing mechanism to explain the emergence of new individuals at other levels or in other contexts. He confusingly embraced the "Lamarckian" label, though not because of any misplaced faith in the inheritance of acquired characteristics. As historian Charlotte Sleigh explains, he only embraced the Lamarckian label because "it was the best label to suit his conviction that evolution was a more holistic and reflexive process than one involving simple individuals" (Sleigh 2004, 152). In one revealing passage, Wheeler distinguished his generation from Darwin's not because they rejected natural selection, but because they embraced cooperation:

> The future historian of science will probably emphasize the difference of attitudes towards the living world exhibited by Darwin and his contemporaries and that of the present generation of twentieth-century biologists. He will notice that the works of the Victorians abound in such phrases as the "struggle for existence," "survival of the fittest," "Nature, red in tooth and claw." [...] We would insist that it depicts not more than half of the whole truth. To us it is clear that an equally pervasive and fundamental innate peculiarity of organisms is their tendency to cooperation, or "mutual aid," as it was called by Prince Kropotkin. (Wheeler 1923, 3)

Wheeler's proclamation was more than just prophetic hyperbole. At research institutions across the United States and abroad, biologists were asking probing questions about the nature of cooperation and its implications for individuals at every level.

Throughout the 1930s, the Biology Department at the University of Chicago housed the most vocal advocates for the multilevel individuality of insect colonies (Mitman 1988). Among the Chicago school, none proved more enthusiastic about both multilevel individuality and emergent evolution than termite expert Alfred Emerson. Like Wheeler, Emerson marveled that the termite colony so closely resembled an individual organism.[5] And, like Wheeler, he called attention to the colony's functional differentiation, as well as its ontogenetic/phylogenetic development. Emerson distinguished himself, however, when he introduced an important wrinkle. In his opinion, the colony was also organismic because it was the target of natural selection. "The important ecological principle of natural selection acts upon the integrated organism, superorganism or population," he wrote (Emerson 1939, 197). This criterion was an important one, for it went well beyond Wheeler's recognition that the colony was a biological individual, and assigned credit to natural selection for demarcating that individual. As historian Pamela Henson explains, "Emerson integrated thinking on homeostasis and equilibrium theory with Darwin's principle of natural selection to develop his theory of biological and social evolution" (Henson 2008, 391).

Emerson (who began his 1939 essay with the same quotation from Kepler that headlines this essay) saw no contradiction between his belief in natural selection and his belief in emergent evolution, though he recognized that his interpretation of the evolutionary process compelled one to rethink traditional criteria for individuality. "Our concept of the individual becomes rather abstract," he acknowledged, adding that "we have to redefine our term as a living entity exhibiting a certain dynamic equilibrium and maintaining a relative stability in time and space." Final-

[5] In fact, Wheeler first used the "superorganism" label in reference to a termite colony, rather than an ant colony (Wheeler 1920).

ly, Emerson understood that his liberal interpretation of the individual applied equally well to all levels of biological organization, from genes to multi-species communities. "These ascending hierarchies of integrated units with their special characteristics form the basis of the concept of emergent evolution," he announced (Emerson 1939, 182).

## Plant ecology and the multi-species individual

Unlike sponges and insect colonies, the multi-species community is a much more recent object of scientific analysis. In 1880, German zoologist Karl Möbius famously identified the oyster community as a distinct ecological unit. As he explained it, "every oyster-bed is thus to a certain degree, a community of living things, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance." He proposed a new word, *biocoenosis*, to describe "a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory" (Möbius 1880, 113). Meanwhile, American biologist Stephen Forbes drew similar conclusions about the interrelationships among disparate species in his landmark essay, "The Lake as a Microcosm" (Forbes 1887). Yet, while both Möbius and Forbes identified the community as a discrete organic entity, neither made any attempt to develop the organismic analogy, nor did either apply the analogy to other systems.

Nebraska ecologist Frederic Clements was the first to forcefully champion the idea that the multi-species community was itself an individual organism. Clements first made explicit reference to the plant community as a "complex organism" in *Research Methods in Ecology* (Clements 1905). Over the next decade, he grew increasingly convinced that the plant community was a dynamic entity persistent in space and time. He believed that the succession of the community revealed a procession, from simple to complex, toward an ideal state of equilibrium known as the climax community. "The general behavior of the formation as a complex organism resembles very closely that of the simple organism, the individual," he wrote. Like the zoologists who identified true organisms at various levels, Clements insisted that the constituent individuals also functioned as organs. "The development of the formation as an organism," he wrote, "is to be found in the responses or functions of the group of individuals, just as the power of growth in the individual lies in the responses or functions of various organs" (Clements 1916, 7). The analogy was strained, however, by the apparent absence of coordinated differentiation (division of labor) among the constituent individuals. In place of functional differentiation, Clements emphasized the similarity between the successional development of a community and the ontogenetic growth of an individual. "The process of organic development is essentially alike for the individual and the community," he wrote. "As an organism, the formation arises, grows, matures, and dies" (Clements 1916, 124). He even referred to the earliest stages of community development as the community's "childhood and adolescence," while he called the climax the "adult" stage because it represented the "highest type of social organism" capable in a given climate (Clements 1935a, 2).

Clements's use of the organism label was somewhat muddled. He largely based his organismic analogy on the similarity between succession and the ontogenetic growth of an individual, which was not at all uncommon. Huxley, Wheeler and Emerson had also cited processes analogous to both ontogeny and phylogeny when demarcating individual organisms at various levels. But calling something organismic is not the same as calling it emergent. Emergence requires novelty borne of its constituent parts' unique coordination. Revisiting Clements's theories at mid-century, Egler expressed pity that "Clements died without having grasped the significance of the concept of holism" (Egler 1951, 692). Egler's position was not entirely fair, however. Though it is true that Clements continued to base his organismic analogy on ontogeny throughout the 1930s, his writings also showed increased sensitivity to his theory's holistic possibilities. After all, the community's status as an organism not only rested upon its ontogeny, but also its homeostasis.

By the late 1930s, Clements had expanded his view of the community organism to include animals. Plant ecology and animal ecology had developed largely independent of one another, and Clements was eager to synthesize (McIntosh 1986, 88). In 1939, he joined forces with Victor Shelford, who had studied under Henry Chandler Cowles at Chicago, served as the first President of the Ecological Society, and was among the nation's leading animal ecologists. Together they published an ambitious textbook, *Bio-Ecology* (1939), in which they insisted that the concept of the organismic community easily allowed animals into the fold. "Animals must also be considered members of the climax," Clements elsewhere explained, proposing the word "biome" to encompass the mutual roles of both plants and animals. He insisted that the biome "is not merely greater than the sum of its constituent species and individuals, but these in turn are something different in the community from what they are when detached from it" (Clements 1935b, 247). What is more, Clements increasingly recognized that coordination played an important role in the evolutionary process, and that "the organization of the family group from the lowest to the highest organisms suggests the extent to which cooperation can be made to overrule competition" (Clements 1933, 36).

While many biologists felt that the idea of a multi-species individual strained credulity, Clements nevertheless found several enthusiastic allies. For example, Julian Huxley was similarly interested in "dissimilar units" that nevertheless ranked as "obvious organic individuals." He cited lichens (which consist of two "botanically very distinct components"), as well as the co-dependent relationship between termites and their intestinal flora, as evidence that true individuals consisting of multiple species do in fact exist. Huxley understood that assigning individuality to multi-species aggregations might prove "difficult to stomach," but he was confident that his multilevel interpretation of the universe rendered just such phenomena inevitable. "If we believe that in the course of evolution individuals of a higher grade have developed by unification of an aggregate of individuals of a lower grade," Huxley reasoned, "we should expect to find cases in which it was impossible to say whether the old individuality of the aggregated parts or that of the system as a whole was the more fundamental" (Huxley 1926, 308-310).

Nor was Huxley the only zoologist who entertained notions of multi-species individuals. Wheeler had readily endorsed the idea as early as 1911, remarking that the multi-species biocoenosis was a true organism (Wheeler 1911, 131). Expanding his thesis during the 1920s, he insisted that the sociality which binds, say, an insect colony, operates on the same principle that governs symbiosis among disparate species. His interest in this "tendency to consociation with strange organisms" stemmed from his observation that many ant colonies played host to a number of foreign species (Wheeler 1926, 437). Intrigued, Wheeler questioned whether one should consider these alien guests, swept up in the colony's "ever-widening-vortex," as part of the superorganism (Wheeler 1923, 172-173). He ultimately decided that they *were* part of the individual, and, furthermore, that these mixed colonies qualified as a "super-super-organism, or superorganism of the second degree" (Wheeler 1926, 437).

Meanwhile, Alfred Emerson was more explicit still. "The same forces which bring about the integration of the organismic units within the species can also be shown to be active in the ecological community," he wrote. He repeated claims about the community's ontogeny and phylogeny, and even argued for its reproductive differentiation. "Individual genes and chromosomes show independent assortment in the history and dynamics of the germ plasm, and thus parallel the independent assortment of germ plasms among the species composing the integrated ecological community," he wrote. Conceding that the bonds uniting the ecological community might appear tenuous, Emerson cited other multi-species individuals in which integration was far more advanced. "The ecological community may exhibit loosely integrated components," he acknowledged, "but such closely integrated relationships as the cellulose-digesting symbiotic flagellates with their roach and termite hosts have a long history indicating greater stability than the 'ageless' mountains." What is more, just as he championed the insect colony in support of multilevel individuality, so too did he utilize the ecological community. "Possibly we should classify ecological associations as ascending levels of super-superorganismic integration which show partial physiological isolation between the community types, and complete isolation only between the biota of this planet and that of some other planet," he remarked with soaring grandiloquence (Emerson 1939, 201).

## Concepts of biological individuality during the Cold War, 1945-1989

Although Huxley, Wheeler, Emerson, Clements and others had thrown their full support behind the idea that cooperative and collective behavior had yielded true individuals at multiple levels of the biological hierarchy, events were already conspiring to undermine their theory's significance. Most notably, the science of genetics, which had developed at the same time as emergent evolution (1920s and 1930s) but entirely distinct from it, had grown increasingly robust. Interested in the smallest components of living things, geneticists dismissed suggestions that biological phenomena, however complex, were somehow irreducible. British geneticist J.B.S. Haldane spoke for many of his colleagues when he remarked that "the extremer forms of the doctrine of emergence are particularly hostile to true scientific progress" (Haldane 1932, 156). The genetic movement gathered additional momentum in 1937, when Theodosius Dobzhansky published *Genetics and the Origin of Species* (Dobzhansky 1937). Synthesizing Darwinian natural selection and Mendelian genetics, the book heralded the dawning of a new age in biology, one that placed far greater emphasis on population genetics (Mayr and Provine 1980; Smocovitis 1992; Ayala and Fitch 1997; Corning 2012). Over the next dozen years or so, several other eminent biologists echoed Dobzhansky's appeals for a more rigorous, quantitative and experimental approach to evolutionary studies (Mayr 1942; Simpson 1944; Stebbins 1950).

It is significant that Julian Huxley, one of the foremost champions of the modern synthesis, never fully surrendered his emergent inclinations. In 1947, by which time the synthesis had already congealed, Huxley reaffirmed his belief that the evolutionary process yields new emergents: "Now and again there is a sudden rapid passage to a totally new and more comprehensive type of order or organization, with quite new emergent properties, and involving quite new methods of further evolution," he wrote (Huxley and Huxley 1947, 120). By that point, however, Huxley was in the minority. Mastery of the atom had just secured victory for the Allied forces, and wholesale faith in neo-reductionism permeated biology no less than physics. What is more, two of the foremost advocates for multilevel evolution, William Morton Wheeler and Frederic Clements, had recently passed away (1937 and 1945, respectively). Emerson continued to promote his multilevel interpretation of emergent evolution following the end of World War II (Allee et al. 1949), but his organicist ruminations were increasingly viewed as passé. Even though Emerson had placed natural selection at the center of emergent evolution, his theory stood little chance in the reductionist fervor then sweeping through the profession.

What the rise of genetics had begun, the discovery of the double helix soon completed. The achievement by Watson and Crick (1953) not only revolutionized the biological sciences, but also fostered "new faith in the reductionist method of the natural sciences" (E.O. Wilson 1994, 225). Theories that had carried the day twenty years earlier now inspired scoffs. After sitting through one of Emerson's lectures on the superorganism in the late 1950s, a young graduate student named George C. Williams left disgusted by what he considered reckless theorizing, and vowed to challenge multilevel interpretations of evolution (Borrello 2010, 107). In 1966, Williams published *Adaptation and Natural Selection*, in which he insisted that group selection was theoretically possible, but that the necessary conditions were almost never present in nature (Williams 1966). Williams's treatise proved enormously influential, and the exclusivity of individual selection was treated as standard textbook fare by the 1970s.

As reductionism took hold of the biological sciences, support for the holistic theories that kept emergent evolution afloat began to evaporate. "In its most strident form," Peter Corning writes, "reductionism swept aside the basic claim of emergent evolutionists that wholes had irreducible properties that could not be fully understood or predicted by examining the parts alone" (Corning 2005, 126). Although the doctrine of emergent evolution explicitly disavowed vitalism, the theory was nevertheless "ejected from mainstream evolutionary studies, as what appeared to be a narrowing or streamlining of evolutionary theory took place" (Smocovitis 1992, 26). Finally, even though Emerson had demonstrated that natural selection and multilevel evolution were entirely compatible, his ideas were dismissed as "naïve." Unable to resist the reductionist onslaught, Henson writes, "Emerson's concept of the 'superorganism' had little long-term impact on a field that was to move away from holistic approaches to research, focusing on more specialized studies" (Henson 2008, 391).

As might be expected, this reductionist spirit quelled talk about the levels of selection in every field of biology, including the ones reviewed in this paper. By the late 1960s, a majority of sponge scientists had agreed that the entire sponge mass constituted a single individual, while those who believed that sponge cells represented true individual zooids were reduced to a "minor" faction. Hartman and Reiswig allowed that sponge cells manifested some measure of individuality, but rejected the suggestion that they were "previously existing zooids [...] reduced to the point that they are unrecognizable (as) the colony has become highly individualized." Instead, they cited embryological, morphological, and cytological evidence as proof that sponge individuality existed at just one level, the metazoan (Hartman and Reiswig 1973, 567).

Even the entomological sciences, so ripe for holistic theorizing, abandoned multilevel theorizing. Theodor Schneirla's report (1944) on the army-ant death vortex spurred new research into the chemical signals that induced such behavior, but these reductionist analyses found little use for multilevel rhetoric. Later, the well-chronicled development of kin selection convinced most entomologists that apparent selection at levels above the metazoan insect was illusory (Hamilton 1964a; 1964b; Maynard Smith 1964). Williams (1966) and Dawkins (1976) both added to the development of gene's-eye thinking, which strengthened the case for reductionism (Okasha 2006). Further, Dawkins (1976) highlighted outlaw genes, which were able to "spread despite their negative effects on the host organism's fitness" (Okasha 2006, 145).

Finally, a majority of ecologists likewise abandoned multilevel interpretations of nature in favor of more reductionist explanations. In 1935, British ecologist Arthur Tansley famously suggested that the vegetative unit should be referred to as a "system" rather than an "organism" (Tansley 1935). Henry Gleason (1939) and Robert Whittaker (1957; 1959) also dismissed organismic analogies in favor of a more individualistic approach.

## Multilevel selection and the declaration of interdependence, 1989 and beyond

If history has taught us nothing else, however, it has taught us that trends are cyclical, and that, in time, what is old is new again. As Bert Hölldobler and E.O. Wilson (an arch-individual selectionist turned arch-multilevel selectionist) once remarked, "Old ideas in science [...] never really die. They only sink to mother Earth, like the mythical giant, Antaeus, to gain strength and rise again" (Hölldobler and E.O. Wilson 1994, 111). The first indication that multilevel selection was not dead appeared in the 1970s, when George Price (1970) convinced William Hamilton (1975) that natural selection could, in fact, target groups of individuals (Harman 2010). Curiously, Hamilton's reversal failed to generate much notice among his colleagues, who did not really begin expressing renewed interest in multilevel selection until, suggestively, the end of the Cold War. Beginning in the late 1980s, however, a small group of biologists and philosophers began promoting a hierarchical interpretation of evolution (Buss 1987; Lloyd 1988; D.S. Wilson and Sober 1989). Since then, a growing number of scientists and scholars have joined them, coalescing around a sweeping theory of life based on notions of multilevel selection.

Perhaps not surprisingly, this renewed interest in the various levels of selection has manifested in each of the fields we reviewed in this paper. For example, contemporary biologists have not only revived many of the old questions about the individuality of the sponge, but have introduced several new lines of inquiry as well. Janie Wulff has shown how a branching sponge that breaks into several noncontiguous pieces yet retains its genomic individuality (Wulff 1991; 1995). Others, like Ruth Ann Dewel, believe that the sponge is crucial to understanding the transition from coloniality to multicellularity, writing that a "colony of cells then 'individuated' into a multicellular 'superorganism' with a sponge level of organization" (Dewel 2000, 62). In similar fashion, Werner G. Müller insists that "the ancestor of all metazoans was a sponge-like organism," and describes the historical process whereby integrated colonies of cells achieved individuation through integration (Müller 2003, 3).

In the entomological sciences, the celebrated revival of the superorganism has also led to increased support for multilevel selection. When Sober and Wilson championed the concept's revival (D.S. Wilson and Sober 1989), social insects were among the exemplars of multilevel selection that they cited. Later that year, Thomas Seeley (1989) proclaimed the honey bee colony a "superorganism," and others soon followed suit (Hölldobler and E.O. Wilson 1991; Southwick and Moritz 1994; Tschinkel 1999). As Sandra Mitchell (1995) points out, however, biologists offered different criteria for the colony's organismic nature. For example, E.O. Wilson initially adopted the metaphor based on functional differentiation, suggesting that parallels between morphogenesis and sociogenesis might prove instructive. Meanwhile, Sober and D.S. Wilson credited natural selection with demarcating the boundary of the individual colony no less than the boundary of the individual ant. In a seismic turn of events, E.O. Wilson (D.S. Wilson and E.O. Wilson 2008; Nowak et al. 2010) recently reversed course on this matter, and now throws his full support behind the latter interpretation.

Meanwhile, multilevel selection remains anathema for many community ecologists, for whom talk of "organisms" and "individuals" harkens memories of strained parallels between ontogenetic growth and successional development. Jonathan Chase and Tiffany Knight hasten to distance their research from the "discredited ideas of Frederick Clements" (Chase and Knight 2003, 579), while Simon Levin is more resolute still. "The ecosystem is not a unit of selection," he recently proclaimed, adding that the "Clementsian view of the ecological community as a superorganism was largely destroyed by the work of Robert Whittaker" (Levin 2005, 1077). Even so, other biologists are perfectly comfortable recognizing multi-species communities as discrete individuals. Concordant with multilevel selection's main tenet, they no longer base their organismic analogies on ontogenetic development, and instead cite the unifying cohesion provided by natural selection. On these grounds, biologists have assigned organismic status to a variety of multi-species associations, including metazoans and their microbial symbionts, leafcutter ants and their fungus gardens, intracellular symbionts, and dual-composite lichens (Sanders 2006; Seal and Tschinkel 2007; O'Fallon 2008; Zilber-Rosenberg and Rosenberg 2008; Gilbert et al. 2012).

Despite its increasing popularity, multilevel selection is not without controversy. It should be noted, for example, that researchers have so far failed to agree on the theory's exact parameters. Some biologists, most notably David Sloan Wilson and Edward O. Wilson, insist that natural selection is sufficient to explain the emergence and maintenance of the various levels of the biological hierarchy, and that other explanations (read: inclusive fitness) are unnecessary. This assertion has met resistance on several fronts, as many biologists object to what they perceive is a false dichotomy. As early as 1984, Alan Grafen complained that arguments distinguishing inclusive fitness and natural selection were "purely didactic – there is no disagreement about matters of substance" (Grafen 1984, 82). James A.R. Marshall agrees. "Despite assertions to the contrary, the group selection and inclusive fitness viewpoints have long been known to be equivalent perspectives on the same process" (Marshall 2011, 329). In similar fashion, Régis Ferrière and Richard Michod both readily acknowledge that natural selection drives "interactions of all kinds and at all levels," but they are unwilling to dismiss the explanatory power of inclusive fitness (Ferrière and Michod 2011, e7).

While some therefore insist that kin selection and multilevel selection provide "equivalent perspectives," still others object that multilevel selection is flat-out wrong. Large numbers of biologists and philosophers continue to insist that natural selection operates only on individuals (by which they usually mean multicellular individuals), while others reject all higher-level selection on grounds that selection operates exclusively on genes. The stakes are high, especially since multilevel selection purports to subsume gene selection. Oxford biologist Richard Dawkins, whose legacy largely rests on his selfish-gene interpretation of evolution, remains particularly intransigent. He recently dismissed multilevel selection as "a bland, unfocussed ecumenicalism," and sneered that it has only found favor among "biologists with non-analytical minds" (Dawkins 2012). Yet Dawkins's objections may prove instructive beyond their intent. Like so many other authors, Dawkins routinely conflates "group selection" with "multilevel selection," but in doing so he overlooks a critical distinction. Multilevel selection does not regard "individuals" and "groups" as fixed categories, but rather context-dependent ones, and this principle applies to genes no less than cells and colonies. After all, what is an individual gene if not a group of biochemical compounds? As Okasha explains, "replicating molecules combining themselves into compartments is strictly analogous to individual organisms combining themselves into colonies or groups" (Okasha 2005, 1015-1016).

This hierarchical structure is one of the heuristic hallmarks of multilevel selection, but the idea is not without precedent. As early as 1911, Wheeler mused that "if the cell is a colony of lower physiological units, or biophores, as some cytologists believe, we must face the fact that all organisms are colonial or social and that one of the fundamental tendencies of life is sociogenic" (Wheeler 1911, 141). Huxley echoed that sentiment fifteen years later, when he noted that "one and the same object may be under one aspect an individual, under another a constituent part of a larger individuality" (Huxley 1926, 318). These sentiments accord surprisingly well with prevailing interpretations of multilevel selection, which portray the levels of selection as Russian matryoshka dolls, each one nested within the next (D.S. Wilson and E.O. Wilson 2008, 380).

Nor is that the only similarity between emergent evolution and multilevel selection. Consider, for example, that many early biologists emphasized coordination as a causative agent in evolution, thereby anticipating more recent trends in evolutionary research (Sapp 1994; Dugatkin 1996; Michod 1999; Traulsen et al. 2009, Nowak and Highfill 2011; Gilbert et al. 2012). It is also telling that many biologists in the early twentieth century believed that "superorganisms" should instead be referred to as "organisms" or, better still, "individuals," a clarifying distinction that many contemporary biologists and philosophers have also stressed (Queller 2000; Strassman and Queller 2009; Martens 2010; Folse et al. 2010). Finally, just as scientists and scholars now describe a new diachronic interpretation of multilevel selection, one that accounts for the major transitions in evolution, so too did earlier biologists ask why any organism would cede part of its individuality to a greater whole, and, moreover, how that higher individual achieves evolutionary stability (Buss 1987; Maynard Smith and Szathmáry1994; Okasha 2005; Calcott and Sterelny 2011).

Acknowledging similarities between the long-dismissed theory of emergent evolution and the increasingly popular theory of multilevel selection need not discredit the latter. After all, the two theories are by no means identical, and many would argue that multilevel selection easily subsumes the same threats (the molecularization of biology, selfish genes, individual selection, kin selection, etc.) that once doomed its predecessor. What is more, supporters of emergent evolution (with the exception of Emerson) failed to provide a convincing mechanism that would apply to the entire biological hierarchy, whereas contemporary biologists now recognize that natural selection provides the impetus for evolutionary change at every level. Finally, but perhaps most importantly, these early-twentieth-century biologists offered no explanation for the infamous "free rider" problem, which researchers now recognize must be overcome if selection is going to forge cohesive groups in which the parts work for the good of the whole.

While contemporary discussions about the nature of biological individuality and the various levels of the biological hierarchy are therefore more nuanced and better quantified than similar debates from a century ago, it is nevertheless significant that many of the ideas now closely associated with multilevel selection first germinated in the oft-ignored early decades of the twentieth century. Biologists from that era are often dismissed on the grounds that they failed to recognize natural selection as the prime agent of evolutionary change. Though it is true that most of them failed to provide a convincing mechanism for evolutionary transitions, it is also true that their ideas have been misrepresented in the historiography, and that they were perhaps not as naïve as their reputations would suggest. After all, these early biologists constructed a multilevel interpretation of evolution that contextualized superorganisms, utilized nested hierarchies, explained major transitions, and emphasized cooperation. What is more, one of them, termite expert Alfred Emerson, artfully united the theory of emergent evolution and the principle of natural selection in a way that is wholly consistent with the theory of multilevel selection being proffered in many academic circles today.

Just as emergent evolution once provided evolutionary biologists with a third option, one that freed them from stagnant debates between materialists and vitalists, so too might multilevel selection now provide modern biologists with a measure of liberation. Acknowledging the biological individual's context-dependency provides a satisfying resolution to the tired debates between reductionists and holists, while emphasizing cooperation provides a compelling alternative to the neo-Darwinian emphasis on competition and atomistic isolation. What is more, the major transitions between levels of individuality are altogether inexplicable without a better appreciation for this coordinating impulse. Indeed, just as Herbert Spencer Jennings (1927) once dubbed emergent evolution a declaration of independence because it secured biology's professional autonomy, so too might one regard multilevel selection as a declaration of *inter*dependence, a shared conviction that cooperation plays a major role in evolution, and that, however discordant life may seem, nature favors harmony no less than conflict.

*Acknowledgments*

Research for this article was funded by a National Science Foundation grant to promote integration between the humanities and the biological sciences. The authors would like to thank Fritz Davis, Chelse Prather, Michael Ruse, Walter Tschinkel, and Janie Wulff for their valuable comments on earlier versions of this article.

## References

Alexander S., 1920, *Space, Time and Deity*, London: MacMillan and Company.

Allee W.C., Emerson A.E., Orlando P., Park T. and Schmidt K.P., 1949, *Principles of Animal Ecology*, Philadelphia: W.B. Saunders Company.

Anker P., 2001, *Imperial Ecology: Environmental Order in the British Empire, 1895-1945*, Cambridge: Cambridge University Press.

Arnold A.J. and Fristrup K., 1982, "The Theory of Evolution by Natural Selection: a Hierarchical Expansion," *Paleobiology*, 8(2): 113-129.

Arp R., 2008, "Life and the Homeostatic Organization View of Biological Phenomena," *Cosmos and History: the Journal of Natural and Social Philosophy*, 4(1-2): 260-285.

Ayala F.J. and Fitch W.M., 1997, "Genetics and the Origin of Species: an Introduction," *Proceedings of the National Academy of Sciences of the United States*, 94: 7691-7697.

Blitz D., 1992, *Emergent Evolution: Qualitative Novelty and the Levels of Reality*, Norwell (MA): Kluwer Academic Publishers.

Borrello M., 2005, "The Rise, Fall, and Resurrection of Group Selection," *Endeavour*, 29(1): 43-47.

Borrello M., 2010, *Evolutionary Restraints: the Contentious History of Group Selection*, Chicago: Chicago University Press.

Bouchard F., 2010, "Symbiosis, Lateral Function Transfer and the (Many) Saplings of Life," *Biology and Philosophy*, 25: 623-641.

Bowler P.J., 1983, *The Eclipse of Darwinism: Anti-Darwinian Theories in the Decades around 1900*, Baltimore: Johns Hopkins University Press.
Brandon R.N., 1990, *Adaptation and Environment*. Princeton: Princeton University Press.
Broad C.D., 1925, *The Mind and its Place in Nature*, New York: Harcourt, Brace and Company.
Buss L., 1987, *The Evolution of Individuality*, Princeton (NJ): Princeton University Press.
Calcott B. and Sterelny K., 2011, *The Major Transitions in Evolution Revisited*, Rochester: MIT Press.
Clarke E., 2012, "Plant Individuality: a Solution to the Demographer's Dilemma," *Biology and Philosophy*, 27: 321-361.
Clayton P., 2006, "Conceptual Foundations of Emergence Theory," in: Clayton P. and Davies P. (eds), *The Re-Emergence of Emergence: the Emergentist Hypothesis from Science to Religion*, New York: Oxford University Press, 1-31.
Clements F.E., 1905, *Research Methods in Ecology*, Lincoln (NE): University Publishing Company.
Clements F.E., 1916, *Plant Succession: an Analysis of the Development of Vegetation*, Washington: Carnegie Institution of Washington.
Clements F.E., 1933, "Competition in Plant Societies," reprinted in: Allred B.W. (ed.), *Dynamics of Vegetation*, New York: H.W. Wilson Company, 1949, 22-37.
Clements F.E., 1935a, "Plant Succession and Human Problems," reprinted in: Allred B.W. (ed.), *Dynamics of Vegetation*, New York: H.W. Wilson Company, 1949, 1-21.
Clements F.E., 1935b, "Ecology in the Human Service," reprinted in: Allred B.W. (ed.), *Dynamics of Vegetation*, New York: H.W. Wilson Company, 1949, 246-278.
Clements F.E. and Shelford V.E., 1939, *Bio-ecology*, New York: Wiley.
Corning P., 2002, "The Re-Emergence of Emergence: a Venerable Concept in Search of a Theory," *Complexity*, 7(6): 18-30.
Corning P., 2005, *Holistic Darwinism: Synergy, Cybernetics, and the Bioeconomics of Evolution*, Chicago: Chicago University Press.
Corning P., 2012, "The Re-emergence of Emergence, and the Causal Role of Synergy in Emergent Evolution," *Synthese*, 185: 295-317.
Damuth J. and Heisler I.L., 1988, "Alternate Formulations of Multilevel Selection," *Biology & Philosophy*, 3(4): 407-430.
Dawkins R., 1976, *The Selfish Gene*, Oxford: Oxford University Press.
Dawkins R., 2012, "The Descent of Edward Wilson," *Prospect Magazine*, May 24. URL: http://www.prospectmagazine.co.uk/magazine/edward-wilson-social-conquest-earth-evolutionary-errors-origin-species/. Accessed March 4, 2013.
Denton J., Kumaramanickavel G. and Legge M., 2013, "Cells as Irreducible Wholes: the Failure of Mechanism and the Possibility of an Organicist Revival," *Biology and Philosophy*, 28: 31-52.
Dewel R.A., 2000, "Colonial Origin for Eumetazoa: Major Morphological Transitions and the Origin of Bilaterian Complexity," *Journal of Morphology*, 243: 35-74.
Dobzhansky T., 1937, *Genetics and the Origin of Species*, New York: Columbia University Press.

Dugatkin L.A., 199, *Cooperation among Animals: an Evolutionary Perspective*, Oxford: Oxford University Press.
Dugatkin L.A., 2006, *The Altruism Equation*, Princeton, N.J.: Princeton University Press.
Egler F.E., 1951, "A Commentary on American Plant Ecology, Based on the Textbooks of 1947-1949," *Ecology*, 32(4): 673-695.
Eldakar O.T. and Wilson D.S., 2011, "Eight Criticisms Not to Make about Group Selection," *Evolution*, 65(6): 1523-1526.
Elwick J., 2007, *Styles of Reasoning in the British Life Sciences: Shared Assumptions, 1820-1858*, London: Pickering and Chatto.
Emerson A.E., 1939, "Social Coordination and the Superorganism," *American Midland Naturalist*, 21(1): 182-209.
Ferrière R. and Michod R.E., 2011, *Inclusive Fitness in Evolution* (471): e6-e7.
Folse H.J. and Roughgarden J., 2010, "What is an Individual Organism? A Multilevel Selection Perspective," *The Quarterly Review of Biology*, 85(4): 447-472.
Forbes S., 1887, "The Lake as a Microcosm," *Bulletin of the Scientific Association* (Peoria, IL): 77-87.
Gardner A., West S.A. and Wild G., 2011, "The Genetical Theory of Kin Selection," *Journal of Evolutionary Biology*, 24(5): 1020-1043.
Gilbert S.F., Sapp J. and Tauber A.I., 2012, "A Symbiotic View of Life: We Have Never Been Individuals," *The Quarterly Review of Biology*, 87(4): 325-341.
Gleason H.A., 1939, "The Individualistic Concept of the Plant Association," *American Midland Naturalist*, 21(1): 92-110.
Goldsby H.J., Dornhaus A., Kerr B. and Ofria C., 2012, "Task-switching Costs Promote the Evolution of Division of Labor and Shifts in Individuality," *Proceedings of the National Academy of Sciences of the United States*, 109(34): 13686-13691.
Goodnight C.J. and Wade M.J., 2000, "The Ongoing Synthesis: a Reply to Coyne, Barton, and Turelli," *Evolution*,54(1): 317-324.
Grafen A., 1984, "Natural Selection, Kin Selection, and Group Selection," in: Krebs J.R. and Davies N.B. (eds), *Behavioural Ecology*, 2nd edition. Oxford: Blackwell Scientific Publications, 62-84.
Haldane J.B.S., 1932, *The Causes of Evolution*, New York: Harper & Brothers.
Hamilton W.D., 1964a, "The Genetical Evolution of Social Behavior I.," *Journal of Theoretical Biology*, 7(1): 1-16.
Hamilton W.D., 1964b, "The Genetical Evolution of Social Behavior II.," *Journal of Theoretical Biology*,7(1): 17-52.
Hamilton W.D., 1975, "Innate Social Aptitudes of Man: an Approach from Evolutionary Genetics," in: Fox R. (ed.), *Biosocial Anthropology*, London: Malaby Press, 133-153.
Harman O., 2010, *The Price of Altruism: George Price and the Search for the Origins of Kindness*, New York: Norton.
Hartman W.D. and Reiswig H.M., 1973, "The Individuality of Sponges," in: Boardman R.S., Cheetham A.H. and Oliver A.O. (eds), *Animal Colonies: Development and Function through Time*, Stroudsburg (PA): Dowden, Hutchinson, and Ross, Inc., 567-384.
Henderson L.J., 1917, *The Order of Nature*, Cambridge (MA): Harvard University Press.

Hölldobler B. and Wilson E.O., 1994, *Journey to the Ants: a Story of Scientific Exploration*, Cambridge: Belknap Press.
Hölldobler B. and Wilson E.O., 2008, *The Superorganism: the Beauty, Elegance, and Strangeness of Insect Societies*, New York: W.W. Norton & Company.
Huxley J.S., 1912, *The Individual in the Animal Kingdom*, London: Cambridge University Press.
Huxley J.S., 1923, *Biology and Society. Essays of a Biologist*, New York: A A. Knopf.
Huxley J.S., 1926, "The Biological Basis of Individuality," *Journal of Philosophical Studies*, 1(3): 305-319.
Huxley J.S. and Huxley T.H., 1947, *Evolution and Ethics 1893-1943*, London: Pilot.
James-Clark H., 1865, *Mind in Nature: the Origin of Life, and the Mode of Development of Animals*, New York: Appleton and Company.
James-Clark H., 1866, "Conclusive Proofs of the Animality of the Ciliate Sponges, and of their Affinities with the Infusoria Flagellata," *American Journal of Science and Arts*, 42: 320-324.
James-Clark H., 1871, "The American Spongilla, a Craspedote, Flagellate Infusorian," *American Journal of Science*, 102: 426-436.
Jennings H.S., 1927, "Diverse Doctrines of Evolution, their Relation to the Practice of Science and of Life," *Science*, 65 (1672): 19-25.
Keller D.R. and Golley F.B., 2000, *The Philosophy of Ecology: from Science to Synthesis,* Athens: University of Georgia Press.
Kim J., 1999, "Making Sense of Emergence," *Philosophical Studies*, 95: 3-36.
Kohler R., 2002, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology*, Chicago: University of Chicago Press.
Korb J. and Heinze J., 2004, "Multilevel Selection and Social Evolution of Insect Societies," *Naturwissenschaften*, 91: 291-304.
Largent M.A., 2009, "The So-Called Eclipse of Darwinism," in: Ruse M. and Cain J. (eds), *Descended form Darwin: Insights into the History of Evolutionary Studies, 1900-1970*, Philadelphia: American Philosophical Society, 3-21.
Levi C., 1999, "Sponge Science, from Origin to Outlook," *Memoirs of the Queensland Museum*, 44: 1-7.
Levin S.A., 2005, "Self-Organization and the Emergence of Complexity in Ecological Systems," *BioScience*, 55 (12): 1075-1079.
Lloyd E.A., 1988, *The Structure and Confirmation of Evolutionary Theory*, Westport, Connecticut: Greenwood Press.
Lloyd Morgan C., 1923, *Emergent Evolution*, London: Williams and Norgate, Ltd.
Marshall J.A.R., 2011, "Group Selection and Kin Selection: Formally Equivalent Approaches," *Trends in Ecology and Evolution*, 26(7): 325-332.
Martens J., 2010, "Organisms in Evolution," *History and Philosophy of the Life Sciences*, 32: 373- 400.
Maynard Smith J., 1964, "Group Selection and Kin Selection," *Nature*, 201(4924): 1145-1147.
Maynard Smith J. and Szathmáry E., 1995, *The Major Transitions in Evolution*, New York: Oxford University Press.
Mayr E., 1942, *Systematics and the Origin of Species, from the Viewpoint of a Zoologist*, Cambridge: Harvard University Press.

Mayr E. and Provine W., 1980, *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, Cambridge: Harvard University Press.
McCoy E.D. and Schrader-Frechette K., 1992, "Community Ecology, Scale, and the Instability of the Stability Concept," *Proceedings of the Biennial Meeting of the Philosophy of Science Association,* Contributed Papers, 1: 184-199.
Michod R.E., 1997, "Cooperation and Conflict in the Evolution of Individuality: Multilevel Selection of the Organism," *American Naturalist*, 149(4): 607-645.
Michod R.E., 1999, *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*, Princeton (NJ): Princeton University Press.
Minchin E.A., 1900, *Sponges – Phylum Porifera. A Treatise on Zoology*, Lankester E.R. (ed.), London: Adam & Charles Black.
Mitchell S., 1995, "The Superorganism Metaphor: Then and Now," in: Maasen S., Mendelsohn E. and Weingart P. (eds), *Biology as Society, Society as Biology: Metaphors*, Norwell (MA): Kluwer Academic Publishers, 231-247.
Mitman G., 1988, "From the Population to Society: the Cooperative Metaphors of W.C. Allee and A.E. Emerson," *Journal of the History of Biology*, 21(2): 173-194.
Mitman G., 1992, *The State of Nature: Ecology, Community, and American Social Thought, 1900-1950*, Chicago: University of Chicago Press.
Möbius K., 1880, *The Oyster and Oyster Farming*, English translation. U.S. Commission Fish and Fisheries Report: 683-751.
Moritz R.F.A. and Southwick E.E., 1992, *Bees as Superorganisms: an Evolutionary Reality*, Springer-Verlag.
Müller W.G., 2003, "The Origin of Metazoan Complexity: Porifera as Integrated Animals," *Integrative and Comparative Biology*, 43(1): 3-10.
Nowak M., Tarnita C.E. and Wilson E.O., 2010, "The Evolution of Eusociality," *Nature*, 466(7310): 1057-1062.
Nowak M.A. and Highfield R., 2011, *Supercooperators: Altruism, Evolution, and Why We Need Each Other to Succeed*, New York: Free Press.
Nyhart L.K. and Lidgard S., 2011, "Individuals at the Center of Biology: Rudolf Leuckart's *Polymorphismus der Individuen* and the Ongoing Narrative of Parts and Whole," *Journal of the History of Biology*, 44(3): 373-443.
O'Fallon B., 2008, "Population Structure, Levels of Selection, and the Evolution of Intracellular Symbionts," *Evolution*, 62(2): 361-373.
Okasha S., 2005, "Multilevel Selection and the Major Transitions in Evolution," *Philosophy of Science*, 72(5): 1013-1025.
Okasha S., 2006, *Evolution and the Levels of Selection*, New York: Oxford University Press.
Osborn H.F., 1894, "The Discussion between Spencer and Weismann," *Psychological Review*, 1: 312-315.
Parker G.H., 1924, "Implications of the Evolutionary Hypothesis," *The Philosophical Review*, 33(6): 593-603.
Queller D.C., 2000, "Relatedness and the Fraternal Major Transitions," *Philosophical Transactions: Biological Sciences*, 355(1403): 1647-1655.
Rosenberg A., 2006, "Biology's Untenable Dualism Or, How to Stop Worrying and Love Molecular Biology," *Darwinian Reductionism*, Chicago: University of Chicago Press.

Ruse M., 1980, "Charles Darwin and Group Selection," *Annals of Science*, 37: 615-630.
Sanders W.B., 2006, "A Feeling for the Superorganism: Expression of Plant Form in the Lichen Thallus," *Botanical Journal of the Linnean Society*, 150(1): 89-99.
Sapp J., 1994, *Evolution by Association: a History of Symbiosis*, New York: Oxford University Press.
Sapp J., 2010, "Saltational Symbiosis," *Theory in Biosciences*, 129(2-3): 125-133.
Schneirla T.C., 1944, "A Unique Case of Circular Milling in Ants, Considered in Relation to Trail Following and the General Problem of Orientation," *American Museum Novitates*, 1253: 1-26.
Seal J.N. and Tschinkel W.R., 2007, "Coevolution and the Superorganism: Switching Cultivars Does Not Alter the Performance of Fungus-Gardening Ant Colonies," *Functional Ecology*, 21: 988-997.
Seeley T.D., 1989, "The Honey Bee Colony as a Superorganism," *American Scientist*, 77: 546-553.
Sellars R.W., 1922, *Evolutionary Naturalism*, Chicago: The Open Court Publishing Company.
Simberloff D., 1980, "A Succession of Paradigms in Ecology: Essentialism to Materialism and Probabilism," *Synthese*, 43(1): 3-39.
Simpson C., 2012, "The Evolutionary History of Division of Labour," *Proceedings of the Royal Society*, 279: 116-121.
Simpson G.G., 1944, *Tempo and Mode in Evolution*, New York: Columbia University Press.
Sleigh C., 2004, "'The Ninth Mortal Sin': the Lamarckism of William Morton Wheeler," in: Lustig A., Richards R. and Ruse M. (eds), *Darwinian Heresies*, New York: Cambridge University Press, 151-172.
Sleigh C., 2007, *Six Legs Better: a Cultural History of Myrmecology*, Baltimore: Johns Hopkins University Press.
Smocovitis V.B., 1992, "Unifying Biology: the Evolutionary Synthesis and Evolutionary Biology," *Journal of the History of Biology*, 25(1): 1-65.
Smuts J.C., 1926, *Holism and Evolution*, New York: The Macmillan Company.
Sober E. and Wilson D.S., 1997, *Unto Others: the Evolution and Psychology of Unselfish Behavior*, Cambridge (MA): Harvard University Press.
Spaulding E.G., 1918, *The New Rationalism*, New York: Henry Hold and Company.
Spencer H., 1881, *The Principles of Sociology*, volume 1, New York: Appleton and Company.
Stebbins G.L., 1950, *Variation and Evolution in Plants*, New York: Columbia University Press.
Strassmann J.E. and Queller D.C., 2010, "The Social Organism: Congresses, Parties, and Committees," *Evolution*, 64: 605-616.
Szathmáry E. and Demeter L., 1987, "Group Selection of Early Replicators and the Origin of Life," *Journal of Theoretical Biology*, 128(4): 463-486.
Tansley A.G., 1935, "The Use and Abuse of Vegetational Concepts and Terms," *Ecology*, 16(3): 284-307.
Tobey R., 1981, *Saving the Prairies: the Life and Cycle of the Founding School of American Plant Ecology, 1895-1955*, Berkeley (CA): University of California Press.

Todes D., 1989, *Darwin without Malthus: the Struggle for Existence in Russian Evolutionary Thought*, New York: Oxford University Press.
Tschinkel W.S., 1999, "Sociometry and Sociogenesis of Colonies of the Harvester Ant," *Ecological Entomology*, 24(2): 222-237.
Voultsiadou E., 2007, "Sponges: an Historical Survey of their Knowledge in Greek Antiquity," *Journal of the Marine Biology Association of the United Kingdom*, 87: 1757-1763.
Wade M.J., 1982, "Evolution of Interference Competition by Individual, Family, and Group Selection," *Proceedings of the National Academy of Sciences of the United States*, 79(11): 3575- 3578.
Wade M.J., Wilson D.S., Goodnight C., Taylor D., Bar-Yam Y., de Aguiar M.A.M., Stacey B., Werfel J., Hoelzer G.A., Brodie E.D., Fields P., Breden F., Linksvayer T.A., Fletcher J.A., Richerson P.J., Bever J.D., Van Dyken J.D. and Zee P., 2010, "Multilevel and Kin Selection in a Connected World," *Nature*, 463(7283): E8-E9.
Watson J.D. and Crick F.H.C., 1953, "A Structure for Deoxyribose Nucleic Acid," *Nature*, 171: 737-738.
Weismann A., 1893, "The All-Sufficiency of Natural Selection: a Reply to Herbert Spencer," *The Contemporary Review*, 64: 596-610.
Wheeler W.M., 1911, "The Ant Colony as an Organism," *Journal of Morphology*, 22: 307-325.
Wheeler W.M., 1918, "A Study of Some Ant Larvae, with a Consideration of the Origin and Meaning of the Social Habit among Insects," *Proceedings of the American Philosophical Society*, 57(4): 293-343.
Wheeler W.M., 1920, "The Termitodoxa, or Biology and Society," *The Scientific Monthly*, 10(2): 113-124.
Wheeler W.M., 1923, *Social Life among the Insects*, New York: Harcourt, Brace and Company.
Wheeler W.M., 1926, "Emergent Evolution and the Social," *Science*, 64: 433-440.
Wheeler W.M., 1928, *Emergent Evolution and the Development of Societies*, New York: Norton and Company.
Whitehead A.N., 1925, *Science and the Modern World*, New York: The Macmillan Company.
Whittaker R.H., 1957, "Recent Evolution of Ecological Concepts in Relation to the Eastern Forests of North America," *American Journal of Botany*, 44(2): 197-206.
Whittaker R.H., 1959, "On the Broad Classification of Organisms," *The Quarterly Review of Biology*, 34(3): 210-226.
Williams G.C., 1966, *Adaptation and Natural Selection*, Princeton: Princeton University Press.
Wilson D.S., 1997a, "Biological Communities as Functionally Organized Units," *Ecology*, 78(7): 2018-2024.
Wilson D.S., 1997b, "Multilevel Selection Theory Comes of Age," *The American Naturalist*, 150(s1): s1-s21.
Wilson D.S., 2011, "Selfless Evolution: a New Consensus," *New Scientist*, 211(2824): i-viii.
Wilson D.S. and Sober E., 1989, "Reviving the Superorganism," *Journal of Theoretical Biology*, 136: 337-356.

Wilson D.S. and Sober E., 1994, "Reintroducing Group Selection to the Human Behavioral Sciences," *Behavioral and Brain Sciences*, 17(4): 585-654.
Wilson D.S. and Wilson E.O., 2007, "Rethinking the Theoretical Foundation of Sociobiology," *Quarterly Review of Biology*, 82(4): 327-348.
Wilson D.S. and Wilson E.O., 2008, "Evolution 'for the Good of the Group'," *American Scientist*, 96: 380-389.
Wilson E.O., 1971, *The Insect Societies*, Cambridge: Belknap Press.
Wilson E.O., 1994, *Naturalist*, Washington D.C.: Island Press.
Wilson H.V.P., 1907, "On Some Phenomena of Coalescence and Regeneration in Sponges," *Journal of the Elisha Mitchell Scientific Society*, 23(4): 161-174.
Wilson J., 1999, *Biological Individuality: the Identity and Persistence of Living Entities*, New York: Cambridge University Press.
Worster D., 1977, *Nature's Economy: a History of Ecological Ideas*, New York: Cambridge University Press.
Wulff J.L., 1995, "Effects of a hurricane on survival and orientation of large, erect coral reef sponges," *Coral Reefs*, 14: 55-61.
Wulff J.L., 1991, "Asexual fragmentation, genotype success, and population dynamics of erect branching sponges," *Journal of Experimental Marine Biology and Ecology*, 149: 227-247.
Wynne-Edwards V.C., 1962, *Animal Dispersion in Relation to Social Behavior*, London: Oliver & Boyd.
Zilber-Rosenberg I. and Rosenberg E., 2008, "Role of Microorganisms in the Evolution of Animals and Plants: the Hologenome Theory of Evolution," *FEMS Microbiology Reviews*, 32(5): 723-735.