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Submitted September 23, 2018; Accepted August 20, 2020; Electronically published October 28, 2020

Online enhancements: supplemental table. Dryad data: https://doi.org/10.5061/dryad.msbcc2fw9.

**Abstract:** The American Naturalist recently passed its sesquicentennial. Throughout this long history, it regularly encountered moments of introspection and debate over its goals, mission, identity, and audience. Here, we chronicle the history of those debates and transitions at critical moments. The Naturalist began as a popular magazine for amateur naturalists in the late 1860s. In the late 1870s, it transitioned to an increasingly academic journal for professional scientists from all branches of the natural sciences. By the turn of the century, academic specialization led to increasing fragmentation of the sciences into a multitude of societies and journals, creating an identity crisis for the once-broad-reaching American Naturalist. This identity crisis was resolved when the journal pivoted around 1910 to focus on fundamental advances in the newly emerging field of genetics. In the 1960s, the journal underwent a remarkably rapid transition to its present focus on evolution and ecology. The profound shifts in the journal’s contents over this time are a reflection of the historical changes in science as a whole: from amateur naturalists, to polymath professionals, to increasingly specialized academics. This chronicle reveals the ways in which The American Naturalist has left its mark on many disciplines, many of which are today only loosely affiliated with the journal, if at all.

Keywords: history of science, American Naturalist, theory.

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Today, The American Naturalist is mostly seen as a publication outlet for evolutionary ecology, sometimes with a theoretical slant. This is not an unfair characterization of the journal, given the articles that have appeared since at least 1980; surveying these recent decades, we see roughly an equal mix of ecology, evolution, and behavior (fig. 1a) and a roughly equal balance of empirical and theoretical articles (or both; fig. 1b). Such a present-day focus, however, represents less than a third of the journal’s history. At more than 150 years of age, it remains the “oldest continuously published American biological journal,” as former editor, geneticist L. C. Dunn, once noted in a brief history more than 50 years ago (Dunn 1966). As one might expect of a journal of such longevity, The American Naturalist has taken dramatic and at times sudden and unexpected directions with changing focus (table S1, available online). Its survival has depended on its ability to capitalize on current movements, broadening, narrowing, and at times changing its focus and scope entirely as other life science journals appeared and disappeared.

The purpose of this article is to study the history of the journal with an eye on these moments of transition to better understand the history of the biological sciences, especially in the United States. The article draws on previous historical work but is primarily based on a close study of the journal itself, including its many editorials, letters, and other non-research-related inclusions as well as its articles. It also draws briefly on the archival record, where it sheds particular light on one of these moments of transition, as well as the history of scientific publications, a relatively new area of study in the history of science (see especially the recent history of the journal Nature in Baldwin 2015). We examine these changes and focus on particular moments of transition by carefully reading each successive journal volume, tracking its editorial policies and successive editors. Fittingly, the changing masthead and motto of the journal reflects changes in editorial policies and
emphases (fig. 2). We argue that these transitions were not arbitrary or capricious but instead often followed what we might view as legitimate “identity crises” that stemmed from the stunning growth and changing trajectories of the biological sciences more broadly (as asserted in the epigraph from L. C. Dunn).

“A Popular Illustrated Magazine of Natural History” (1867–1878): The Founding of the Journal and the American Society of Naturalists (ASN)

The initial masthead or motto, quoted in the heading above, appeared on the cover page of the earliest issues of The American Naturalist, just below the journal’s name (fig. 2, upper left). It might be surprising to current readers to see it as a mere “popular magazine,” given its technical nature today; but peer review was virtually nonexistent until the very late nineteenth century, started coming into wider use in the 1930s, and became convention only during the Cold War (Baldwin 2018). The emphasis on natural history reflected dominant currents in the sciences, broadly construed, which included subjects such as anthropology, archaeology, and geology, along with more traditional domains of the life sciences. During the Reconstruction period in the United States (named after the Reconstruction Acts of 1867) after the end of the Civil War, science went through a period of rapid intellectual growth and institutionalization, placing new emphasis on research (Olsen and Voss 1979). Land-grant universities, for example, boomed in the wake of the Morrill Act of 1862 that launched them, as did experiment and field stations, institutes, gardens, and museums, all devoted to generating new knowledge, both basic and applied. These changes created a professional class of scientist (the term was coined only in 1833), increasingly educated in the United States rather than Europe. These professionals began to dominate what had been primarily the amateur study of the natural world (e.g., this transition in ornithology is described in Barrow 1998).

The journal’s start was also built on theoretical developments made apparent by the publication of Darwin’s On the Origin of Species in 1859 (just 8 years earlier), which drew attention to the lawlike regularities in the natural world, highlighted the importance of empirical observation as well as experimentation, and provided a framework for understanding the growing field of natural history. Scientific expeditions were also revealing more about global biological diversity, and interest was increasingly turning to the study of the native flora and fauna of the United States undergoing extinction (Barrow 2009; Brinkman 2010). With the growth of a middle-class reading public, interest in natural history in the United States was peaking around the time of the founding of the journal, as was nature study, which was becoming part of school curricula (Kohlstedt 2010). In short, the context was ripe for the appearance of a popular illustrated newsmagazine that could appeal

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**Figure 1**: Recent publishing emphasis of *The American Naturalist*. (a) Relative abundance of article topics from 1980 until 2017. D. I. Bolnick categorized articles, on the basis of their titles, from the first three issues of every fifth year from 1867 through 2018. Here, we plot just the proportions of the 114 articles from this sample of issues from 1980 onward. (b) Present-day ratios of articles (from the 2017 volumes) focused on empirical data, theoretical models, or a fusion of the two. Data are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.msbcc2fw9; Bolnick et al. 2020).
to the increasing interest in the natural world and be sold to a wide readership.

The brief four-page introductory to the first volume described its appearance in terms of a “utilitarian age.” The stated goal was to produce “a scientific monthly addressed to all lovers of nature” that “will be equally welcome to farmers, gardeners, and artisans” and whose aim was “practical and economic as well as theoretical,” closely matching the ideals of the newly emerging land-grant universities. The new editors hoped to “awaken the absorbing interest by the contemplation of nature, and of illustrating the goodness and wisdom of the Creator, than on any

Figure 2: Front pages of The American Naturalist from 1867, 1882 (Darwin’s obituary), 1909, 1946, 1951, and 1977, showing the different mottoes and moments of key transition highlighted in this history. Photographs from Mark McPeek, thanks to the Museum of Comparative Zoology at Harvard University.
adornment of style, or cunning devices of the artist." This statement reflects the natural theology movement, which viewed contemplation of nature as confirmation of God's design. The magazine thus targeted popular audiences, but it also created space for those also interested in understanding the "origin of life" through secondary laws as well as those favored by the "followers of Lamarck or Darwin" (quotations from vol. 1, pp. 1–4).

Details of the early days of the journal are described more fully in published historical articles, including several concerning the early history of *The American Naturalist* (Editors 1877; Minot 1902; Conklin 1934, 1944; Dexter 1956; Dunn 1966). To summarize these briefly, the first issue appeared in March 1867 and was published by four former students of Swiss naturalist and Harvard professor Louis Agassiz (1807–1873). Alpheus Packard (1839–1905) was an entomologist who described more than 500 species, mostly of butterflies. Frederick Putnam (1839–1915) was an archeologist now widely regarded as the "father of American archaeology." Edward Morse (1838–1925) was a polymath whose work spanned zoology and anthropology, while Alpheus Hyatt (1838–1902) was a Civil War veteran who specialized in zoology and paleontology. All four were denied permanent appointments at Harvard, where they chafed under the "tyrannical" personality of Agassiz, who strictly dictated their research activities (see Lurie 1960). The four formed a "Society for the Protection of American Students from Foreign Professors" and left Harvard for the Peabody Academy of Science and the Essex Institute in Salem, Massachusetts, where they began to publish *The American Naturalist*. The journal was not affiliated with any scientific society; the ASN was founded 6 years later.

The initial publication was received with great enthusiasm from naturalists as well as more practically minded farmers and gardeners. Packard wrote to his father and noted that "it's selling like hot cakes!" (Dexter 1956). The first printing of 1,000 issues sold quickly, and for the second volume 2,500 copies were printed. Subscriptions included public libraries, which would reach the wide audience they targeted, and not just academic institutes and university libraries.

Some examples provide us with a sense of some of the journal's early style. The articles were on the one hand practical: a letter writer commended the editors for an 1867 article on the natural history of locusts, saying that it should be required reading for farmers in Kansas (Dexter 1956). Others were anecdotal and strangely chatty, to our modern sensibilities. Noted botanist Charles Wright (1811–1885), for instance, wrote "A Comical Owl" in 1868 about the behavior and diet of a young Cuban owl he adopted: "The owl is called a solemn bird. It may be so; yet I have seen one in Cuba whose actions would upset the gravity of a very sober meeting. . . . His power of swallowing was surprising." A similarly colorful description came from Lucie L. Hartt, the first woman to publish in *The American Naturalist*; she told the story of a cephalopod grabbing her hand while she was exploring a tide pool in Brazil (Hartt 1869). And in what became a kind of signature piece for the magazine, the songs of various species of grasshoppers were written out in musical form for readers (Scudder 1868). The articles were often accompanied by detailed original engravings and illustrations, to both delight and inform.

Not all of the articles had this lighthearted tone, however. For example, Mary Treat (1830–1923), who is known for her prolific contributions to botany and entomology (she published 76 articles and five books, and she corresponded extensively with Darwin), wrote articles on experimental tests of sex determination in butterflies (Treat 1873). The journal also featured serious descriptions of new species and new fossil finds (e.g., Marsh 1873). A particularly notable example of the latter was by Louis Agassiz (the editors' estranged mentor), who used geological observations in the White Mountains of New Hampshire to propose a recent glacial epoch (Agassiz 1870), now known as the Pleistocene. Agassiz published this and only two other articles in *The American Naturalist* before dying in 1873, just a few years after the journal's founding.

"Devoted to the Natural Sciences in Their Widest Sense" (1879–1908): Professionalization

In 1877, the journal underwent the first of its major transitions after Edward Drinker Cope (1840–1897) bought a half share of it and became its editor. He dropped the term "popular" (as well as "magazine") from the title and increasingly used it to publish broadly in the natural sciences. This transition reflected the growing number of professional scientists. The British journal *Nature*, which was also founded as a popular news magazine 2 years after *The American Naturalist*, underwent similar professionalization around the same time (Baldwin 2015).

Cope's purchase of the journal was not entirely selfless. *The American Naturalist* had been the primary venue for acerbic and personal exchanges with his archival, Othniel Charles Marsh (1831–1942), who fought against him in the celebrated Bone Wars (for just two accounts of this feud, see Wallace 1999; Jaffee 2000). Their exchanges got so bad that by 1873, readers appealed to the editors: "Editors, keep these 'scientific lights' in this healthy air, and do not allow them to sink below the average plane of our 'commercial, literary, or religious papers.' 'Scientific thought' is too dignified for such expressions as 'misrepresentation,' or 'efrontery,' 'criminally,' 'ambiguous,' or 'untrue'" (as cited in Dexter 1958). After acquiring the journal in 1877, Cope used his position to publish much of his own work.
(750 of his 900 articles appeared in these pages) without interference from his nemesis.

Despite Cope’s own focus on paleontology, under his editorship the journal published articles from every corner of the natural sciences: geology and paleontology (e.g., Cope 1894), biochemistry (Ward 1882; Abbott 1887a, 1887b), embryology (Morris 1883; King 1902), immunology (Claypole 1894; Nuttall 1901), ethnology (Chever 1870), archaeology (Rau 1883), heredity (Bodington 1895), zoology (Sanger 1884), systematics (Hill 1883a), botany (Hill 1883b), and behavior (Caton 1883; Platt 1899), among many other topics. Where these articles touched on evolution, they adopted the neo-Lamarckian stance that was typical of Agassiz’s students and contemporaries. Some articles fell outside the boundaries of science as we define it today (e.g., “Hypnotism in Animals”; Prentiss 1882) but reflected Victorian preoccupations.

This period also saw the first tentative steps toward garnering an international audience. One of the founders, Edward Morse, traveled to the University of Tokyo in Japan and established collaborations with zoologist Kakichi Mitsukuri (1857–1909) and his students. To our knowledge, an 1883 article by Chiyomatsu Ishikawa (1861–1935), a zoologist who introduced Darwinian evolution to Japan, is the first publication in the journal by an author outside Europe and North America.

Despite increasing professionalization, many contributors were intellectual polymaths by today’s standards. This was certainly true for a number of women contributors who could not be employed full time as scientists but who nevertheless remained active at publishing (for details, see Bronstein and Bolnick 2018). For example, Alice Brooke Bodington (1840–1897), who was more of a science writer than professional scientist, wrote ethnological analyses of legends (Bodington 1893); descriptions of parasites inhabiting tumors (Bodington 1894); essays on the heredity of insanity, especially in royal families (Bodington 1895); and two articles on the evolution of the human mind (Bodington 1892a, 1892b). The last are shockingly racist. Her assertions about the inferiority of “primitive” or “savage” people reflected the dominant beliefs of evolutionary anthropologists in late nineteenth-century America as well as Europe, and they were closely aligned with Cope’s own writings on white supremacy (Davidson 1997). Yet another prolific contributor, Emily Lovira Gregory (1840–1897), published more focused pieces on the comparative dimensions of German versus American schools of plant physiology and had the distinction of being elected the first woman in the ASN in 1886, although not as a charter member (Gregory 1892a, 1892b).

Throughout Cope’s reign as editor, most articles were descriptive natural history, broadly defined. But some publications were very prescient conceptual advances that shaped our modern views of biology. It would come as some surprise to today’s subscribers that one of the most profound and important articles in The American Naturalist was the discovery of blood types. In 1901, George Nuttall (1862–1937) described experiments showing that “antibodies” form in the blood after exposure to unrelated individuals and different species. Impressively, the author anticipated the use of blood typing in medicine (e.g., for transfusions), forensic science, and even phylogenetics (Nuttall 1901). An equally prescient but lesser-known pair of articles were by Helen Abbott (1857–1904), who posited that evolutionary ideas could be applied to understand plant chemistry (Abbott 1887a, 1887b). Although she was widely respected, her ideas never gained much traction at the time, and her articles were largely forgotten until their recent rediscovery (LoPresti and Weber 2016).

The success of the journal and the increasing number of professionals studying natural history in the United States drew together a group of individuals in 1881 to found an official society, led by invertebrate zoologist S. F. Clarke (1858–1921). In 1883, the Society of Naturalists of the Eastern United States held its first meeting, with 109 charter members. The society subsequently adopted The American Naturalist as its official publication in 1885 and changed its name to the American Society of Naturalists a year later, to reflect its growing geographical span of its members. The ASN was unique in that it was the first of the societies to restrict membership to professionals through its constitution, “limited to Instructors in Natural History, Officers of Museums and other Scientific Institutions, Physicians, and other persons professionally engaged in some branch of Natural History” (Minot 1902).

As with the journal, the ASN did not have a strict disciplinary focus and soon began to lose members to spin-off specialized societies. These included the Association of American Anatomists (1886), the American Physiological Society (1887), the American Morphological Society (later the American Society of Zoologists; 1889), the Geological Society of America (1889), the American Psychological Association (1892), the Botanical Society of America (1893), the Society of American Bacteriologists (1899), and the American Society of Zoologists (1903). (See the list in Conklin 1934.) Historian Toby Appel (1988) described the ASN as an intellectual “halfway house, that by its existence, encouraged the formation of disciplinary societies and enabled them to survive their early years,” an innovation incubator for newly emerging disciplines. This bleeding off of society members was reflected in changing publishing priorities of the journal, as new “daughter” societies started their own, more specialized journals (see also Benson and Quinn 1990; Smocovitis 2006).

Edward Drinker Cope died in 1897, and his estate sold the journal to other Agassiz pupils. The new editor was
zoologist Robert Payne Bigelow (1863–1955), who was concerned with the lack of focus in the journal and its wide scope. In January 1898 he wrote, “From the range of subjects . . . it may be supposed by many that the magazine is to be a kind of scrap basket for a miscellaneous lot of articles which, for one reason or another, have failed to find space in the journals of the special sciences to which they rightly belong. This is what we most earnestly desire to avoid. We wish to select our articles so the magazine shall have a definite character. . . . What common point of view shall cement its diverse departments into a harmonious whole?” His answer was inspiring, although still rather vague: he aspired to publish “a closer union of the natural sciences based not upon superficial observations and poorly grounded speculations, but upon a deeper insight into the real facts. It is the purpose of the American Naturalist to aid and encourage this movement. We desire that our pages afford a common meeting-ground where the morphologist, the physiologist, the zoologist, the botanist, the anthropologist, the palaeontologist, the geologist, and the mineralogist may meet to discuss the problems in which they have a common interest” (Bigelow 1898).

Under Bigelow’s watch, the journal diversified not only in subject matter but also in authorship. Charles Henry Turner (1867–1923) is, to our knowledge, the first African American author in the Naturalist, publishing an article on freshwater ostracods (Turner 1899). Now considered a pioneer in insect behavior, Turner was teaching at Clark Atlanta University, a historically African American college at the time. Although he later earned his PhD from the University of Chicago, he was unable to obtain a faculty position and published most of his research (>70 articles) while teaching high school and serving as a leader of the civil rights movement in Saint Louis (Abramson 2010).

Despite Bigelow’s ambition and energetic interventions, topics of broad common interest that spoke to a diverse community proved elusive. The process of specialization and fractionation only continued. The Geological Society of America was founded in 1889, and within the decade pure geology articles were rare in the Naturalist; even paleontology, which had been so much a centerpiece of the journal for many years, dwindled thereafter (fig. 3a). Anthropological articles dwindled after 1902, when the American Anthropological Association was founded (fig. 3b).

Figure 3: Examples of the exodus of some disciplines from American Naturalist articles. a, Declining proportions of articles on paleontology (solid circles, solid line) and geology (open circles, dashed line). b, Declining prevalence of anthropology (including culture, linguistics, archaeology, and physical anthropology), coinciding with the establishment of the American Anthropological Association. D. I. Bolnick examined article titles from the first three issues of every fifth year, from 1867 through 2018, and counted the number of articles in various categories of study. The 5-year sampling scheme revealed some periods of very rapid transition into and away from genetics. To zoom into these crucial times, we retroactively added data on the first three issues of every year during 1900–1920 and 1950–1970. Lines are splines fit in R (smooth.spline function with 5 df).
The biggest blow came from the ascension of Science as the dominant venue for general interest science, news, and currents of thought, filling the generalist niche that Bigelow and others had envisioned for the Naturalist. Science had started out as a financially troubled and irregularly published popular illustrated magazine. In 1900, however, the American Association for the Advancement of Science (AAAS) formally adopted Science as its primary publication and began to publish articles of wider interest along with the news of other scientific societies. Indeed, a series of essays in Science starting in 1902 discussed the history of The American Naturalist, its goals, and its future directions as it determined what its relationship should be with Science and the AAAS (Minot 1902). The American Naturalist effectively ceded the generalist field to Science and explicitly narrowed its focus.

“Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution” (1909–1947): From Natural History to Genetics

At the start of the twentieth century, both the society and the journal were losing influence, caught between Science’s generalist strategy and the emerging specialist journals (Huxley 1942; Bowler 1983; Allen 1979a). For example, the AAAS largely ignored the ASN when planning 1909 celebrations of Darwin’s 100th birthday and the fiftieth anniversary of the publication of On the Origin of Species. The ASN’s secretary, zoologist H. McE. Knower, expressed dismay at ASN’s exclusion; given that the topic was “peculiarly the province of naturalists . . . there should be no danger of encroachment on the dignity, power or function of naturalists” (Knower 1908). A month later, geneticist and eugenicist Charles Davenport (1866–1944) wrote, “It is argued by those who regard the Society of Naturalists as an anachronism that natural history is no more, that in the differentiation and specialization that accompany the development of science it has broken up into botany, zoology, etc. and that these special sciences are each amply provided for, by at least two organizations.” The solution was to explicitly acknowledge the de facto trend in the journal: “Except in its early years it has been, as it now is, almost exclusively a biological society” (Davenport 1908).

The fate of the society—and the journal—were therefore actively being discussed when the journal was purchased by James McKeen Cattell (1860–1944), a psychologist at Princeton University, who also owned Science. The journal was to remain his family’s business for six decades. Cattell was close friends with experimental zoologist Thomas Hunt Morgan (1866–1945; ASN president in 1903), who was just beginning his famous studies to understand the mechanism of Mendelian heredity in Drosophila melanogaster in his “fly room” at Columbia University. Cattell asked Morgan to become editor of The American Naturalist, and Morgan agreed because it would provide a convenient publication venue for his growing and prolific research team. Morgan’s strong interest in heredity and evolution thus set the direction for the journal, capitalizing on the nascent field of genetics.

Morgan’s interests were reflected in the changing priorities of the ASN as a whole. After the 1908 Baltimore meeting of the ASN, the society announced in a 1908 report in Science that the “main object of the society be considered the study of evolution of its many-sided aspects (historical, environmental, experimental, etc.). There is no subject which would so well hold together all the present members (including botanists, zoologists, physiologists, anatomists, paleontologists, anthropologists, etc.) . . . This temporary plan has now become the settled policy of the society, evolution being properly interpreted to include genetics, cytology and chemistry, as well as the more usual fields of speciation, adaptation, distribution and in general the philosophy of the natural sciences” (Conklin 1944; see also Anonymous 1908). Thus, the ASN set in motion one of the first unifying arguments for the centrality of evolution. Interestingly, the ASN considered genetics in a subordinate role, a subfield of evolution.

Almost immediately, the Naturalist stopped publishing descriptive botany and zoology articles, which had for so long defined the journal (fig. 4a), and published genetics articles instead (fig. 4b). The declining role of natural history in this journal was soon followed by the founding of the American Journal of Botany in 1914 (Smocovitis 2014). The name Mendel first appeared in a single sentence, 3 years after the rediscovery of Mendel’s article. A 1903 article summarizing recent events noted, “Mendel’s law is discussed by Professor Spillman in the Popular Science Monthly for January.” The second mention of Mendel was an April 1904 synopsis of a Royal Society report by William Bateson (1861–1926) and Edith Saunders (1865–1945; Bateson and Saunders 1902). Bateson is well known especially for his advocacy of Mendelian genetics, while Saunders is largely forgotten, although she made notable contributions to plant genetics at the turn of the century and was one of the first women elected to the Linnean Society (for more on Bateson and Saunders, see Richmond 2001). The Naturalist summary was attributed to C.B.D., likely referring to Charles Benedict Davenport. This report (C.B.D. 1904) called their work “the first extensive post-Mendelian account of hybridization experiments in animals” and “epoch-making,” giving particular credit to the experimental work by “Miss Saunders.” The review introduced readers to Bateson and Saunders’ new terminology, which included words like “allelomorph,” “heterozygote,”
The third mention of Mendel was in a 1906 review of geneticist Reginald C. Punnett’s (1875–1967) "popular exposition about experimental crosses. Like Bateson, Punnett relied heavily on Saunders’ data in developing his analyses, and they copublished extensively. The first empirical article on the topic argued that human sex determination could not be explained by Mendelian laws (Pike 1907). The next year a *Naturalist* article reported data on the inheritance of which thumb is dominant in clasped hands (Lutz 1908), including a data table that is still handy for teaching genetics.

Under Cattell’s ownership and Morgan’s editorship, from 1910 through the 1930s the majority of articles in the journal were focused on genetics, often with little or no evolutionary content. Genetics remained a focus of the *Naturalist* even as competing specialist journals appeared: the *Journal of Heredity* in 1903, the *Journal of Genetics* in 1910 (Bateson’s initiative), and *Genetics* in 1917. The *Naturalist*’s table of contents during this interval of time reveals a remarkable set of genetics studies. In 1910, 3 years after the *Naturalist*’s first original article on Mendelian genetics, the journal published a number of articles contributing foundational ideas in modern genetics. In January, Thomas Hunt Morgan published his classic article “Chromosomes and Heredity” (Morgan 1910). This was followed quickly by Edward Murray East’s (1879–1938) classic article reconciling Mendelian and quantitative genetics, "A Mendelian Interpretation of Variation That Is Apparently Continuous" (East 1910). The next year, Wilhelm Johannsen (1857–1927) introduced readers of *The American Naturalist* to the terms “gene,” “genotype,” and “phenotype” (Johannsen 1911). In quick succession Morgan published foundational ideas, including sex-limited and sex-linked inheritance (Morgan 1914b), sex determination (Morgan 1911), and mutagens (Morgan 1914a). An interesting historical sidenote is that Nobel laureate Barbara McClintock (1902–1992) published her first scientific article in *The American Naturalist* (Randolph and McClintock 1926). Many of the findings of the early articles were later falsified, of course. For example, Johannsen (1911) scornfully rejected Morgan’s claims that chromosomes were hereditary elements: “That discrete particles of the chromosomes are ‘bearers’ of special parts of the whole inheritance . . . have no support in experience . . . a purely speculative morphological view of heredity without any suggestive value.”

Although genetics was the primary focus of the *Naturalist* during this period, the journal continued to publish articles on evolution (fig. 5) and other topics. Morgan did not initially endorse Darwin’s view of selection, but his increasing focus on Mendelian genetics changed his mind (Allen 1979b). Noteworthy early twentieth-century
antieugenics stance. The eugenicist articles, it also frequently supported a stridently racist worldview. But while the journal published numerous racist and eugenicist articles, it also supported a stridently anti-eugenics stance. The first article to use the word “eugenics” in its text is actually a blistering critique of the notion "modern synthesis" of evolution, especially Julian Huxley (1887–1975), Theodosius Dobzhansky (1900–1975), and Ernst Mayr (1904–2005), began to argue that “evolutionary biology” (as it was increasingly called) was a distinct discipline, albeit one linked to genetics (Smocovitis 1996). They began to form a number of new organizations bringing together geneticists, systematists, and paleontologists, and in 1946, just after the end of the war, they launched the Society for the Study of Evolution (SSE), with the goal of promoting "the study of organic evolution and the integration of the various fields of biology, such as taxonomy, paleontology and genetics that are interested in evolution." In 1947, this international society introduced a new journal, Evolution.

Because Evolution and The American Naturalist were so close in scope and membership, the newer society threatened to drain members away from the ASN and readers away from the Naturalist, as had happened with geology, anthropology, and other disciplines before. As chronicled in Smocovitis (1994), the new society generated friction and anxiety as the two groups negotiated their relationship. Some of the more enthusiastic members of the SSE proposed an entire takeover of the older journal, preferably by joint agreement between the two societies. Geneticist H. J. Müller (1890–1967), for example, feared that many would probably give up the older journal and society, leading to its demise. He wrote Ernst Mayr, the chief organizer of the new society and first editor of Evolution, "Should the attitude of the new Society be one of artificial aloofness as though Naturalists did not exist, despite the greatly overlapping membership, etc., allowing the Naturalists to gradually wither away, or should they, if they are willing, be accepted into some kind of association or merger?" (H. J. Müller to E. Mayr, June 7, 1948, as cited in Smocovitis 1994).

Such a takeover was aided by the fact that the Naturalist’s long-standing owner, J. McKeen Cattell, had died. He bequeathed Jaques Cattell Press to his sons, Jaques and Ware Cattell, whose commitment to The American Naturalist was uncertain. Indeed, the Cattell brothers offered to sell it to the SSE for $4,000. It never came to fruition because of opposition from two fronts. Ernst Mayr rejected the offer, adamant that it was too much money merely to keep the "undesirable" name of The American Naturalist. Insect taxonomist and sexologist Alfred Kinsey (1894–1956) argued that many ASN members were not even interested in evolution and complained that the Naturalist mostly existed "primarily to make money for the owners" (as cited in Smocovitis 1994). On the other side, some ASN members defended the unique value of the ASN and its journal.

When the SSE declined to purchase The American Naturalist, Ware Cattell took over acting as both owner

**Figure 5:** Relative abundance of articles concerning evolution, by year, in The American Naturalist. Data were collected and splines fit as described in figure 2.

- **“Advancement of the Biological Sciences” (1946–1951): The Evolutionary Schism**
  - Although the journal’s focus on genetics led to the publication of foundational work, it also generated dissatisfaction from contributors who felt excluded. Things came to a head in the late 1930s and 1940s, largely as a result of the growing number of scientists contributing to the fusion of Darwinian selection theory with Mendelian genetics in a populational framework to explain the origins of biological diversity (Mayr and Provine 1980). The architects of this “modern synthesis” of evolution, especially Julian Huxley (1887–1975), Theodosius Dobzhansky (1900–1975), and Ernst Mayr (1904–2005), began to argue that “evolutionary biology” (as it was increasingly called) was a distinct discipline, albeit one linked to genetics (Smocovitis 1996). They began to form a number of new organizations bringing together geneticists, systematists, and paleontologists, and in 1946, just after the end of the war, they launched the Society for the Study of Evolution (SSE), with the goal of promoting "the study of organic evolution and the integration of the various fields of biology, such as taxonomy, paleontology and genetics that are interested in evolution." In 1947, this international society introduced a new journal, Evolution.
  - Because Evolution and The American Naturalist were so close in scope and membership, the newer society threatened to drain members away from the ASN and readers away from the Naturalist, as had happened with geology, anthropology, and other disciplines before. As chronicled in Smocovitis (1994), the new society generated friction and anxiety as the two groups negotiated their relationship. Some of the more enthusiastic members of the SSE proposed an entire takeover of the older journal, preferably by joint agreement between the two societies. Geneticist H. J. Müller (1890–1967), for example, feared that many would probably give up the older journal and society, leading to its demise. He wrote Ernst Mayr, the chief organizer of the new society and first editor of Evolution, "Should the attitude of the new Society be one of artificial aloofness as though Naturalists did not exist, despite the greatly overlapping membership, etc., allowing the Naturalists to gradually wither away, or should they, if they are willing, be accepted into some kind of association or merger?" (H. J. Müller to E. Mayr, June 7, 1948, as cited in Smocovitis 1994).
  - Such a takeover was aided by the fact that the Naturalist’s long-standing owner, J. McKeen Cattell, had died. He bequeathed Jaques Cattell Press to his sons, Jaques and Ware Cattell, whose commitment to The American Naturalist was uncertain. Indeed, the Cattell brothers offered to sell it to the SSE for $4,000. It never came to fruition because of opposition from two fronts. Ernst Mayr rejected the offer, adamant that it was too much money merely to keep the "undesirable" name of The American Naturalist. Insect taxonomist and sexologist Alfred Kinsey (1894–1956) argued that many ASN members were not even interested in evolution and complained that the Naturalist mostly existed "primarily to make money for the owners" (as cited in Smocovitis 1994). On the other side, some ASN members defended the unique value of the ASN and its journal.
  - When the SSE declined to purchase The American Naturalist, Ware Cattell took over acting as both owner
and editor. In 1946 (vol. 80), he articulated a new editorial policy broadening the journal’s scope to be a news source spanning the biological sciences: “There is a great need of integration in biological fields. This will be aided by increasing mutual understanding through the presentation of the progress of new developments, including those of special interest to the biologist in political and international matters. The American Naturalist will have served its purpose well by rallying the forces representing biologists of the country and by serving as the mouthpiece that can be quoted by newspapers at large.” In 1948, the masthead and motto were changed to “A Bi-Monthly Journal Devoted to the Advancement of the Biological Sciences.”

“Devoted to the Advancement and Correlation of the Biological Sciences” (1951–1977)

In 1951, the Cattells finally approached the ASN and asked it to take responsibility for the journal’s scientific content. The January 1951 issue was the first published under the official supervision of the society. The masthead of the journal was soon changed to reflect the new arrangement, stating in 1952 that it was “edited in the interest of the American Society of Naturalists.” Despite this change in management, the journal continued to focus on publishing genetics, often without even a nod toward evolution and certainly no ecology. To illustrate the genetics focus: in 1954 an issue was devoted wholly to the effects of radiation on chromosomes and mutations, as was another in 1960, and in 1961 Barbara McClintock (1902–1992) published an important article on gene regulation (McClintock 1961).

In a remarkably rapid shift, ecology almost completely replaced genetics in the span of just 5 years in the early 1960s (fig. 4b). The shift to ecology coincides with a change in editorial policy near the end of Vernon Bryson’s (1913–) term as editor (1961–1964), just before Richard Lewontin (1929–) took on the position (1965–1968). The following announcement was published in 1964: “The American Naturalist is a bimonthly journal devoted to furthering the objectives of The American Society of Naturalists, which are the ‘discussion, advancement and diffusion of knowledge concerning the broader biological problems, including organic evolution, thus serving to correlate the various biological sciences into a common philosophy of biology.’ It will publish those general addresses, essays and papers presented at the symposia of biological societies which contribute to the above purpose; research papers and reviews in which theoretical interpretation and synthesis are predominant; and brief discussion, criticism and comment on material is published in this journal and elsewhere.” There is no specific mention of ecology here and we know of no documents stating an editorial intention to shift in that direction, but the emphasis on theory and synthesis fit well with growing interest in the synthesis of ecology, evolution, and genetics, as well as with the growing emphasis on theory in ecology.

Ecology had certainly been present in the journal’s pages for decades already. The first references to “ecology” in article titles appear around the same time as Mendelian genetics, with such titles as “Ecology of the Willow Cone Gall” (Heindel 1905), “Research Methods in Ecology by F. E. Clements” (G.M.A. 1906), “Floral Ecology” (Harris 1907), and “The Trend of Ecological Philosophy” (Cowles 1909). Thereafter, references to ecology appeared sporadically, a few each year. Even as late as the 1950s an entire year could pass with no articles using the word “ecology,” although some influential articles did appear, such as Falconer’s (1952) presentation of a theory on how an organism’s environment affects selection on genetically correlated characters.

In 1958, G. E. Hutchinson (1903–1991) gave his presidential address to the ASN, which was published a year later: the celebrated article “Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals?” (Hutchinson 1959). It became a clarion call to many ASN members to take up the question of coexistence, species richness, and biological diversity. It helped to launch an entire movement that brought ecologists together with evolutionary biologists and population geneticists, initiating the merged field of evolutionary ecology (reviewed in Futuyma 1986, 2013). The charge was led by theoretical ecologist Robert H. MacArthur (1930–1972), who first published in the Naturalist with Hutchinson in 1959 and 1960 and remained a prolific contributor until his death. Within 10 years, many foundational articles in ecology had appeared in the journal’s pages (table S1).

MacArthur wrote a series of highly influential articles in the Naturalist that caught the imagination of many aspiring ecologists, who followed MacArthur’s lead by publishing their best work in this journal. Eric Pianka (1939–), MacArthur’s only postdoc, explained, “I started grad school at the University of Washington in 1960. We had an exceptional group of grad students and we devoured MacArthur’s articles—each time a new one came out, we all read it and met in small groups to discuss it. The American Naturalist quickly became our favorite journal” (personal communication to D. I. Bolnick). Pianka adds an interesting anecdote, that MacArthur favored the journal for a very pedestrian reason: he hated revising articles and was known to tear up and discard articles that required extensive changes. He preferred submitting to The American Naturalist because its editors rarely asked for revisions (another aspect of the journal that has changed).
The rise of Hutchinson-MacArthur–style evolutionary ecology in the 1960s coincided with a major shift in research methods to incorporate mathematical theory. As far as we can tell, the first equations appeared in the journal in the first decade of the twentieth century. Durnford (1907) used some simple mathematics of wing geometry to examine the gliding abilities of flying fish. Raymond Pearl (1909) described growth curves in mathematical form. But to our surprise, the quantitative innovations of the evolutionary new synthesis did not make extensive inroads in this journal. The rise of theory (analytical derivations and, more recently, numerical solutions and simulations) was concomitant with the burgeoning of ecological articles that began in the 1960s (fig. 6) and has persisted as a major feature of the journal ever since, with approximately half of published articles containing some element of quantitative theory. Of course, this shift was not exclusively MacArthur’s doing. Richard Levins (1930–2016) presented theory on how multiple ecological niches can sustain genetic polymorphism (Levins 1963). Thomas Park (1908–1922) and Monte Lloyd (1928–2000) in 1955 and then David Pimentel (1925–2000) in 1961 arguably laid the groundwork for what is today called “eco-evo dynamics” (Park and Lloyd 1955; Pimentel 1961). And the influential green world hypothesis (Hairston et al. 1960) began a decades-long obsession with trophic cascades.

Mirroring the rise of theory in the journal, the Journal of Theoretical Biology was founded in 1961, Mathematical Biosciences in 1967, Theoretical Population Biology in 1970, and the Journal of Mathematical Biology in 1974.

Two other practical changes in this period are worth noting. First, starting in January 1966 (vol. 100), the journal began charging authors ($10 per page). At the time, subscription fees brought in only enough to allow up to 380 pages per year to be printed; page charges would allow expansion of the journal. In an editorial announcing this policy in the March–April 1965 issue, the editorial board emphasized that unfunded authors would be helped: “No author, inside or outside the United States, who would otherwise submit a paper, should hesitate to do so because he [sic] does not have funds available for publication costs” (p. 65; italics in the original). The second major change was in 1967: after six decades of managing the journal, the Cattell family planned to cease publishing it. As recounted in box 1, the journal was purchased by the not-for-profit University of Chicago Press, which has managed the publication on behalf of the ASN ever since. This arrangement is increasingly unusual, as many other societies have let large for-profit publishing companies manage their publications.

“Devoted to the Conceptual Unification of the Biological Sciences” (1977 to Today)

The present-day masthead and motto of The American Naturalist, adopted in 1977, echoes its long history of publishing across all sciences—and all of biology in particular. In practice, the journal is narrower, focused on the mix of evolution, ecology, and behavior (fig. 1a) that emerged from the 1960s and has remained relatively steady for a half century. Likewise, the mixture of empirical and theoretical has persisted since the 1960s. Of course, this broad-brush equilibrium obscures many of the finer-grained changes in specific biological questions and new tools that emerged. Arguably, the most notable of these was the 1985 publication by Joseph Felsenstein (1942–), which provided the motives and methods for the massive proliferation of phylogenetic comparative studies (Felsenstein 1985). But many areas of biology are omitted altogether. In particular, the journal has been slow to assimilate the large changes from the genomics era.

Many other changes have taken place in the broader realm of academic publishing: the Naturalist has led in some and been wary of others. A 2005 National Science Foundation–supported meeting of scientific societies explored data archiving and was attended by Managing Editor Patricia Morse. Starting in 2008, Editor Mike Whitlock worked with Morse to develop procedural details. In 2010, multiple journals signed a joint statement calling for data archiving (Whitlock et al. 2010), which The

Figure 6: Proportion of published articles that include quantitative theory, including analytical derivations and simulations. These include articles with a mixture of theory and empirical work. C. M. Moore surveyed the first three issues of every fifth year, as previously. A spline fit is provided, as in the preceding figures.
Box 1: How The American Naturalist came to the University of Chicago Press

The story of the survival of The American Naturalist is in part the story of people who have stepped up to save the journal at critical junctures. In 1967, those people were Richard C. Lewontin and William K. Baker, the editors. Lewontin and Baker had just edited a special issue to celebrate the 100th anniversary of the journal when they learned that the survival of the journal they had just celebrated was in doubt. When the owners of the journal, Jaques and Elizabeth Cattell, had retired, they had sold off their larger and more profitable publishing endeavors. They continued to publish the Naturalist in their retirement, typesetting it on a VariTyper in their living room and handling the details of getting it to the 2,200 subscribers themselves (Dunn 1967; Sacks 1975). Elizabeth Cattell had carried on after Jaques’s death in 1960 but realized that it was too large an enterprise for her to handle alone. She contacted the American Society of Naturalists (ASN) and asked them to purchase the journal (Lewontin and Baker 1966). The ASN at that time was an honorary society with a membership limited to 500. A ballot went out to the members, who voted 349 to 5 to purchase the journal (Lewontin and Baker 1967). There was, however, a problem. The ASN had no money. The treasurer’s report of 1966 shows an income of $1,658 (Russell 1967). Lewontin and Baker searched for a grant (Lewontin and Baker 1967), but by the autumn of 1967 it was clear that they would have no success before Elizabeth Cattell ceased operations with the December 1967 issue.

In the autumn of 1967, Lewontin and Baker were teaching at the University of Chicago, which had a university press to publish scholarly journals. The visionary first president of the university, William Rainey Harper, had founded the university as a research institution and believed that the research it generated needed to be published. He directed the graduate schools and graduate departments to create journals that would be published by the university’s own press. Therefore, when Lewontin and Baker realized that their efforts to find a grant had run out of time, they sprinted across the quadrangles (as dramatically recounted by witness Robert Shirrell; personal communication, May 2001) to ask the University of Chicago Press to step in.

In 1967, the Press still published only University of Chicago–based journals (University of Chicago Press 1967). Acquiring the Naturalist would break a 70-year-old tradition. In addition, all publications at the Press had to be approved by a board of university faculty, and this one entailed a considerable cost. Lewontin and Baker had to persuade their colleagues from across disciplines that a journal “devoted to furthering the objectives of the American Society of Naturalists” (Lewontin and Baker 1967) was worth the university’s investment. Their pitch was made to the October 10, 1967, meeting of the faculty board. Lewontin and Baker put considerable effort into their pitch, compiling extensive lists of the journal’s greatest articles, providing a defense of the journal, and bolstering it with their considerable curriculum vitae. Lewontin and Baker succeeded, although apparently it was a hard sell. After the editorship moved on to the State University of New York at Stony Brook and Lewontin moved on to Harvard, the faculty board again raised the question of why the Press was publishing a journal that was not based at the University of Chicago (Sacks 1975).

The university bought the journal from Elizabeth Cattell in the nick of time. The January 1968 issue rushed to production, with a new masthead statement: “Published for the American Society of Naturalists by the University of Chicago Press.” The transition from Elizabeth Cattell’s living room to the largest university press in the United States and home of the Chicago Manual of Style was not, however, without a hitch. As Lewontin and Baker reported to the ASN in 1968, the relationship was “satisfactory.” However, “the new publishing arrangements have meant somewhat more work for the editors and the editorial assistant since very much more detailed copy editing is now done on manuscripts and an added stage of production—page proofs—must be handled. . . . Thus, the changeover to the University of Chicago Press has made us a little more fussy” (Lewontin and Baker 1969).

The American Naturalist began to require in 2011 for all new submissions. Initially, there was significant resistance from the community, mostly over concerns about other researchers analyzing publicly accessible data in ways that may eclipse the original researchers’ follow-up articles. Submissions to The American Naturalist (and several other journals) did decline when this policy was first introduced. Within a decade, most journals had adopted data-archiving requirements both for greater transparency and repeatability and to enable future reanalyses. A second major change was the adoption of double-blind reviewing in January 2015, by Editor-in-Chief Judith Bronstein. This change emerged from a Women in Science workshop at the 2014 Evolution meeting and sought to minimize bias that may affect reviewers’ judgment, whether conscious or unconscious. Once again, The American Naturalist was one of the first journals in organismal biology to adopt this policy.
Other changes in publishing have been treated more cautiously. Many journals have shifted to entirely online digital publishing. While an electronic article option is available, many authors still opt to appear in the printed version. Many journals have opted for shorter and shorter formats, which often encourage authors to gloss over key details. Although competition for printed space remains keen, the journal continues to consider longer-format articles. Former Editor Mark McPeek put it this way: American Naturalist articles should be as long as they need to be to make their point clearly, and not one word longer. Many journals have increasingly demanded fast turnaround on reviews. The American Naturalist prides itself on thorough review, so it continues to give reviewers the courtesy of time to do a careful and constructive job. 

The University of Chicago Press’s careful copyediting is also a point of pride but entails costs that other journals have dispensed with in shifting to pay-to-publish open access policies. The journal has therefore maintained a hybrid strategy of encouraging authors to pay for open access articles when they can afford it while relying on subscription income to subsidize the many authors who cannot.

Where Next?
The American Naturalist has a long history of foundational contributions to diverse disciplines. One metric of this impact is the many words in our scientific lexicon that originate in its pages: the Oxford English Dictionary lists 463 cases where the journal published the first instance of a word and 1,106 cases of the first use of a word in its modern sense. These include such diverse terms as “cell culture” (1874), “imaginal disc” (1874), “mutualist” (1874), “metazoan” (1876), “nitrogen fixation” (1893), “phylogeny” (1899), “mutant” (1903), “gene” (1909), “heterozygotic” (1911), “phenotypic” (1911), “microevolution” (1911), “ectotherm” and “endotherm” (1940), and “isocline” (1963). The question facing today’s American Naturalist community, its editorial board, authors, and readers is how to sustain the journal’s value to suit its storied history.

If the history of the journal, as outlined above, is any guide, then it can best serve its role by welcoming diverse new lines of inquiry. It should serve as the incubator for new ideas and questions that may grow to be new subfields. Today, the lines between biological disciplines are blurring. Cell and molecular biologists are rediscovering evolution and ecology. Oncologists are increasingly grappling with the consequences of evolution within tumors (Ben-David et al. 2018). Microbiologists studying the gut microbiome are drawing on ideas of community assembly, metacommunities, and other ideas from our field (Costello et al. 2012). Epidemiologists and public health researchers rely on ecological tools and phylogenetic analyses. If The American Naturalist can help blur these lines further, it will be serving our goal of unifying the biological sciences and become the “common meeting ground” for diverse biologists, as envisioned by the journal’s early editor, Robert Bigelow, more than a century ago. This will require an effort to bring in articles drawing on more diverse fields of biology, including more mechanistic studies, physiology, genomics, computation, and medicine, tied together by the broad organizing principles of life that ecology and evolution have laid out over the past half century.

The risk of such a meeting ground is that the journal may appear to be, as Bigelow put it, “a dumping ground for a mismatched assortment of papers.” On the contrary, we would argue that the Naturalist does have a theme. We seek to publish articles that change the way readers think about a topic in organismal biology. Ideally, articles in the journal should contain novel insights or ideas of interest not just to people in the same subdiscipline but to a broader readership. They should lead the reader to say to themselves, “Hmm, I hadn’t thought of that before” or “Here’s evidence for that long-suspected hypothesis.”

This meeting ground is where theoreticians publish articles that should push empiricists to ask new questions and where empiricists should publish observations and data that will inspire new theory. The meeting ground is where evolutionary biologists can continue to present their work for ecologists to read, and vice versa, but also where other disciplines can learn from, and contribute to, both fields.

Acknowledgments
We thank Judith Bronstein (editor, 2014–2017) for her feedback during the development of this article, which is a fusion of lectures given by the authors at Asilomar meetings of the American Society of Naturalists (V.B.S. in 2014; D.I.B. in 2018). Two anonymous reviewers provided valuable feedback.

Statement of Authorship
D.I.B. collected the data and analyzed the data on subject matter trends. C.M.M. collected data on the use of theory in the journal’s history. D.I.B. and V.B.S. jointly planned and wrote the article, with history of theory contributions from C.M.M. P.L.M. contributed box 1 and detailed feedback on the manuscript.

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The accompanying illustration is a restoration of *Hesperornis regalis*. . . . It is a cretaceous bird with teeth, and Professor Marsh on fresh examination finds some additional characters of importance of the order Odontornithes, of which it is a type.’ From “Recent Paleontological Discoveries in the West” (*The American Naturalist*, 1877, 23:500).