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The diversification of developmental biology



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ABSTRACT

In the 1960s, “developmental biology” became the dominant term to describe some of the research that had previously been included under the rubrics of embryology, growth, morphology, and physiology. As scientific societies formed under this new label, a new discipline took shape. Historians, however, have a number of different perspectives on what changes led to this new field of developmental biology and how the field itself was constituted during this period. Using the *General Embryological Information Service*, a global index of post-World War II development-related research, we have documented and visualized significant changes in the kinds of research that occurred as this new field formed. In particular, our analysis supports the claim that the transition toward developmental biology was marked by a growth in new topics and forms of research. Although many historians privilege the role of molecular biology and/or the molecularization of biology in general during this formative period, we have found that the influence of molecular biology is not sufficient to account for the wide range of new research that constituted developmental biology at the time. Overall, our work creates a robust characterization of the changes that occurred with regard to research on growth and development in the decades following World War II and provides a context for future work on the specific drivers of those changes.

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1. Introduction²

In 1959, the United States-based Growth Society published the first issue of the journal *Developmental Biology*. Its publication marked a growing trend in which the label ‘developmental biology’ became the common descriptor for societies, departments, and publications that had previously described themselves using

monikers such as ‘embryology’ and ‘growth’.³ For example, in England, the London Embryologists’ Club changed their name in 1964 to the ‘Society for Developmental Biology’ and added ‘British’ to the beginning once the Growth Society in the United States changed their name to the Society for Developmental biology in 1965 (Slack, 2000).⁴ In the east, the U.S.S.R. Academy of Sciences formed the Institute for Developmental Biology in 1967 (Dettlaff & Vassetzsky, 1997; Korochkin, Konyukhov, & Mikhailov, 1997), and in Japan, the

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² In this article, we will abbreviate the *General Embryological Information Service* as *GEIS*.

³ We do not mean to imply that this is the first time that the name ‘developmental biology’ or a similar variant was used to describe the field. We merely point out that it was not until the late 1950s that the label became a more prominent descriptor of the discipline.

⁴ Though they had precedence, the British biologists modified their society name because the American society was both bigger and was already publishing *Developmental Biology* (Slack, 2000).

Japan Society for Experimental Morphology (1942) and the Embryologia Society (1950) merged in 1968 to become the Japan Society of Developmental Biologists (Okada, 1994). During that same year, the longest standing international organization for the field, the Institut International d'Embryologie (IIE), renamed itself the International Society of Developmental Biologists (ISDB) (Palmeirim & Aréchaga, 2009; Slack, 2000). By the end of the 1960s, 'developmental biology' had become the term *du jour* for the sciences dedicated to understanding growth and development.

In the inaugural issue of *Developmental Biology* in 1959, the founding editor Paul Weiss claimed that the journal title highlighted the universality of growth and development throughout biology. "In the past, development and growth have been dealt with mostly in separate and relatively isolated compartments, such as embryology, or plant physiology, or nutrition, or oncology," Weiss wrote (Weiss, 1959, p. ii). "Yet in reality, all of these are isolated aspects of one continuous spectrum of phenomena, varied manifestations of the same basic principles and elementary processes." The term *developmental biology*, Weiss claimed, "promoted the confluence and integration of related, but formerly isolated, lines" (Weiss, 1959, p. ii). Weiss' 1959 introduction puts forward two different arguments for the adoption of this new label. First, that the term 'developmental biology' lays claim to a broader swath of topics than the more narrow labels of 'embryology' or 'growth'. Secondly, that these previously disparate topics are interrelated at a more fundamental level, meaning that the study of any of these broader concerns of development should theoretically help in understanding all aspects of the field.

Clement Markert, who was President of the Society for the Study of Growth and Development when it changed to the Society for the Study of Developmental Biology in 1964, recalled slightly different reasons for the change in a letter to Evelyn Fox Keller. According to Markert, the name change "was motivated by two reasons: (1) the Growth Society had declined somewhat so that it did not have a very good image; and (2) and more important, the term 'growth' was not descriptive of the Society. The term [developmental biology] was much more descriptive than any previously used term, such as growth or embryology, and did, in fact, enhance the scientific image of the Society in an appropriate fashion" (Keller, 1995, p. 25). In 1961, Peter Nieuwkoop also noted the increasing "specialization with the field of embryology, especially where it borders upon genetics, biochemistry, and biophysics." For Nieuwkoop the shift from the Section of Embryology to the Section of Developmental Biology in the International Union of Biological Science represented "a change indicating an extension of its activities to the entire field of biology" (Nieuwkoop, 1961, 269). Significantly, Weiss, Markert, and Nieuwkoop all had a sense that developmental research had outgrown earlier labels.

Since that period, historians and biologists have debated how the study of development—however it was labeled—actually transformed during this period. Was this simply a semantic change or did diversification and growth of research support a broader label? If there were substantive changes in the fields of growth and development, how can historians best describe them? Were there major intellectual changes at the time? Or were these label changes motivated by new social, institutional, or cultural needs?

To the authors of this paper, the increased use of the moniker "developmental biology" coincides with a period of transformative change in research related to growth and development. As our survey of historical interpretations in the next section shows, many scholars have put forward explanations for the changes that have taken place between World War II and the 1980s in these fields. However, the types of evidence that historians have used to support their explanations has been limited; these explanations have often

been predicated upon studies that involved too narrow a view of topics, people, or geographic areas. Given that some sort of significant change in the study of development occurred during this period of time—which is signaled by the rebranding of the field around the world—our goal in this paper is to try to characterize what changed in the study of growth and development in the years immediately preceding the widespread adoption of the disciplinary label of developmental biology.

Using a much more extensive data set than has previously been applied, we find patterns of change in research growth and diversification of research topics that preceded the nomenclatural turn toward developmental biology. We are not claiming that these changes caused biologists to adopt the term "developmental biology" for their discipline, or that most biologists would have been fully aware of these global patterns of change and research diversification. Instead, we claim that global patterns of growth and diversification in developmental research characterize this period of discipline re-formation, and that these patterns set a new challenge for historians to explain the drivers of this growth and diversification—whether those drivers turn out to be semantic, intellectual, economic, institutional, social, or cultural. In the secondary literature, the most prevalent explanation for this change in the name of the field focuses on the impact of molecularization as a potential driver of change, but given our data and analysis, we find this explanation to be insufficient.

For our broader perspective, we analyze a robust set of post-World War II research data preceding the period in which the term 'developmental biology' increased in popularity. Specifically, we analyzed the *General Embryological Information Service (GEIS)*, an international periodical published from 1949 to 1980, that indexed not only scientists working on topics related to embryology, but also described what research they were conducting. From this data, we can begin to delineate the broader field that the new term 'developmental biology' supposedly encompassed. What we have found in our broad analysis is that there was substantial and increasing research diversification, both in the number and type of research projects before and during the period in which developmental biology became the dominant label for the field. Our goal in this paper is to articulate these patterns of diversification.

For historians, *GEIS* offers a remarkable amount of data about the field focused on growth and development during the middle of the twentieth century. The first issue collated nearly 700 names from scientists at 245 institutions, and by 1980 the editors published the names of over 3400 biologists at 1,200 institutions throughout fifty countries (Palmeirim & Aréchaga, 2009). The figures collected in these volumes represent the majority of practicing scientists focused on biological growth and development during this period, making the topical data that the *GEIS* editors assembled highly indicative of the state of the science during any given volume.

One of the most distinctive and useful aspects of *GEIS* is not the list of names, but rather the catalog of research projects. Specifically, *GEIS* editors required that scientists report *what they were actually doing in the lab* and specifically asked them not to provide bibliographic data of recent publications. As scientists are well aware, not all research conducted in the laboratory gets published. Some projects never succeed, or lead the researcher down dead-ends. Though the scientists may have spent countless hours working in a particular area, the fact that they never published anything from the work means that their efforts are often lost to the historical record. The requirement of *GEIS* editors to report research rather than publication data provides insight into what scientists actually spent time investigating during our period of interest.

These characteristics of *GEIS*, we believe, offer historians the ability to do some large-scale evaluation of the discipline that has not previously been attempted. Often histories of biology, and those interested in development in particular, have focused on the most significant names in the field. Just as social historians have argued since in the 1960s, however, it is important to understand the rank-and-file scientist when trying to articulate the changing nature of a discipline, particularly one as large as the one that became known as developmental biology (Kessler-Harris, 1997; Shapin, 1989). Since *GEIS* included a large number of biologists, and not just those from an Anglo-American context, we believe that analyzing the *GEIS* publications provides us with the best and most comprehensive source of information with which to characterize the field during this period.

That being said, we are aware of the limitations of this data source. The *GEIS* was created and collated by individuals and organizations with their own agendas. Obviously, the biases of the *GEIS* creators could influence how complete the representation of researchers was from different locations and which areas and topics were represented in their research classification. However, because the *GEIS* collected and contained such an impressive number of practicing scientists from a wide range of institutions and countries, we are confident that this data set is the best available way to analyze the research related to growth and development during this period. Knowing the limitations of the *GEIS* means that we have avoided questions regarding the demarcation of boundaries for what was or was not considered embryology and/or developmental biology at a particular time. Instead, we have accepted the terms provided in the *GEIS* and used the data that the *GEIS* offers to characterize the general patterns of change.

By applying some basic visualization and mathematical tools to data extracted from the *GEIS*, we have discovered important changes in the kinds of research that occurred after World War II as the field moved toward its new configuration as 'developmental biology'. In particular, our analysis supports the claim that this period of transition was marked by growth in new topics and forms of research. As we will discuss in the next section, several historians have already tried to articulate the major trends in post-World War II research on development. Although many of these historians privilege the role of molecular biology and/or the molecularization of biology in general during this formative period, we have found that the influence of molecular biology is not sufficient to account for the wide range of new research that mutually informed the new discipline of developmental biology.

2. Historical interpretations

Though historians have written on many aspects of the history of embryology and developmental biology, most of this work has concentrated on the nineteenth and early twentieth centuries as well as specific national contexts (Churchill, 1991a, 1991b; Hamburger, 1988; Harwood, 1993; Hopwood, 2015; Maienschein, 1983, 1986, 1991a, 1991b; Nyhart, 1994). Some, however, have continued their narratives past World War II or have discussed specific trends in the field that influenced the second half of twentieth century (Gilbert, 1994; Gurdon & Hopwood, 2000; Hopwood, 2009; Maienschein, Glitz, & Allen, 2005). In particular, the relationships between embryology and genetics (Burian, 2004; Burian, Gayon, & Zallen, 1994; Gilbert, 1988, 1998; Sapp, 1987;) and embryology and evolution (Amundson, 2000; Amundson, 2007; Churchill, 1980; Hamburger, 1980; Laubichler & Maienschein, 2009; Laubichler & Rheinberger, 2004; Love & Raff, 2003; Robert, 2004) have been the primary foci of historians. A few historians and historically minded biologists, however, have discussed issues

related directly to our questions about the changing nature of the field during the middle of the last century.

Historians Tim Horder and Paul Weindling proposed that around the time of the Second World War the study of development underwent a transformative change from a narrow set of issues associated with embryogenesis and experimental embryology to a much more diverse set of topics and issues associated with the process of development and so called developmental biology (Horder, Witkowski, & Wylie, 1986). They claim that "the term 'developmental biology' became a clarion call to embryologists to create a discipline to rival 'cell' or 'molecular biology,' but also an expression of the broadening of the interests of members of the discipline and the need to maintain links" (Horder & Weindling, 1986, p. 229). Horder and Weindling's interpretation of the transition from embryology to developmental biology emphasizes the way in which developmental biology fit into larger organizational shifts going on throughout biology, particularly the emergence of molecular biology and cell biology.

Horder and Weindling documented this transformation and diversification by following the content from the late 1930s to the early 1950s of the Growth Symposia, an annual symposium organized by the Growth Society (which eventually changed its name to the Society for Developmental Biology in 1965). They noted that induction and research on organizers dominated the earliest meetings, but by 1946 induction had been relegated to one paper with the rest applying other techniques and articulating a range of different theoretical issues (Horder & Weindling, 1986, p. 228). In their words, "what had happened, to put it in the broadest terms, was a swing from the perspective of the whole organism to a growing realization that the potentialities of individual cells encompassed and might explain, the phenomena previously studied in the organism" (Horder & Weindling, 1986, p. 229). Because Horder and Weindling were engaged in writing a history of Hans Spemann's contributions to embryology, they framed this transformation in terms of the turn away from Spemann's research on induction toward cellular and molecular signaling. At the same time, they also acknowledge a "fragmentation of interests," as new subspecialties were created, which often "centered on the use of technically increasingly demanding material, such as the chick and later mammalian embryos" (Horder & Weindling, 1986, p. 229; see also Deichmann, 1996, p. 31).

Other historians have focused more on the integration of molecular biology and molecular thinking as the major instigator of the transition between the two labels. In their introduction to a special issue devoted to this topic, entitled "From Embryology to Developmental Biology," Richard Burian and Denis Thieffry (2000) note the change that Horder and Weindling tried to explain; however, they described the transition simply as the integration of molecular tools and approaches into the traditional study of embryos. For Burian and Thieffry, as well as the rest of the authors in their special issue, the changes in developmental biology reflected what they called "second reorganization of biology," reflecting the 'molecularization of biology,' which they claim was well underway by 1950 (Burian & Thieffry, 2000, p. 316). Burian and Thieffry use the term 'molecularization' broadly here to mean the growing infatuation with biological molecules and cellular materials, rather than a more narrow definition of protein-RNA-DNA interactions one could associate with the term. In doing so, their definition encompasses the rise of macromolecular biochemistry in the middle of the twentieth century (Kohler, 1982), not just the discovery of DNA's structure and the elucidation of the central dogma. As a specific example, Bernardino Fantini (2000a) argues in this special issue that the chemical embryology studies of the 1940s and 1950s by researchers such as Jean Brachet encouraged and precipitated the transition to the molecularization of development-

focused research by the 1960s. Similarly, Soraya de Chadarevian (2000) and Michel Morange (2000a) emphasize in their separate papers the role of early molecular biologists such as Sydney Brenner and Francois Jacob, each of whom worked on developmental systems in the 1960s and are seen by the authors as major contributors to the molecularization of the discipline. Overall, the theoretical thrust of this special issue was that reductionist approaches and molecular biology in particular drove changes occurring in developmental biology after WWII.

One other important historian, Nick Hopwood, has maintained a similar, but more nuanced, articulation of what happened to embryology and developmental biology after the Second World War. Hopwood claims that the adoption of the word 'developmental biology' in the 1960s was "a joint initiative of self-consciously 'modern' embryologists and geneticists, biochemists, cell biologists, and molecular biologists who saw a field ripe for their skills" (Hopwood, 2009, p. 309). For Hopwood, this meant not a redirection of the century-old questions that motivated descriptive and experimental embryology, but rather the application of new tools and approaches to these research projects. For instance, Hopwood relates how in the 1970s future Noble Prize winners Christiane Nüsslein-Volhard and Eric Wieschaus used the contemporary techniques of gene cloning to tackle a classic developmental genetics problem that experimental embryologists had been unsuccessful at solving for decades (Hopwood, 2009, p. 310). Hopwood also notes that in the post-World War Two world the perceived failure of embryology, which supposedly maintained a propensity towards vitalism and holism in the face of reductionist successes, motivated many biologists to reform the discipline, which contributed to the rebranding of embryology as developmental biology (Hopwood, 2009, p. 310).

There is dispute, however, about whether developmental biology effectively integrated the new molecular, biochemical, and genetic approaches of the in the 1960s and 1970s. For the 25th (1964) and 50th (1989) anniversaries of the Symposium for Developmental Biology, two historically minded developmental biologists reflected on how the discipline had changed over their lifetimes. Writing first, Jane Oppenheimer (1965) claimed that since the beginning of the Growth Symposia in 1939, the field had successfully integrated biochemistry, genetics, and macromolecular studies. In contrast, for the 50th anniversary edition of the symposium, Donald Brown (1993) dismissed this idea, saying that Oppenheimer's description of developmental biology did not come to fruition until the 1980s. Rather, developmental biology was previously an "intellectual backwater," and "from the 1930s into the 1960s developmental biology was isolated, with its own theories, methods, and even experimental animals" (Brown, 1993, pp. 1–2). Whereas Oppenheimer's assessment of the field supports the arguments that Burian and Thieffry advanced, Brown's assertions articulate a developmental biology that was outside the fads that swept the rest of biology—in this case, molecular biology. Additionally, Brown's words reflect the type of disdain that new biologists had towards the field, which Hopwood noted in his articulation of the transition during this period.

Overall, one of the most significant issues at stake in the histories of developmental biology after World War II is the articulation of how the molecular revolution of the 1950s maps on to the changing identity politics of developmental biology taking place at the same time. As Horder, Weindling, Burian and Thieffry all noted, there was a broader reorganization of biology in the 1950s and 1960s. Much of this reorganization occurred by way of newly constructed disciplines, which many histories have been have focused on, particularly when it comes to the emergence of molecular biology (Abir-Am, 1985; de Chadarevian, 2002; de Chadarevian & Rheinberger, 2009; Kay, 1996, 2000; Morange,

2000b; Rheinberger, 2009; Sapp, 1990), cell biology (Bechtel, 2008; Maienschein, 1991b), and evolutionary biology (Mayr & Provine, 1998; Smocovitis, 1996).⁵ Taken as a whole, histories of this period of biological reorganization highlight a number of different factors that affected the disciplinary construction of these fields. Historians who have looked at the emergence of developmental biology have done so using the models of how molecular biology, cell biology, and evolutionary biology materialized. Part of our larger goal is to articulate the rise of developmental biology on its own terms rather than assuming that the same mechanisms that produced these other disciplines also apply to developmental biology.

It is also important to point out that historians have not been the only ones who have tried to analyze the changing character of the science surrounding growth and development during the middle of the twentieth century. In 1949, Paul Weiss, a leading developmental biologist, convinced the National Research Council to create the Committee on Developmental Biology to "encourage research in certain areas of developmental biology that tend to be neglected" (Report of the National Academy of Sciences, 1949, p. 77). Weiss organized a series of conferences in the 1950s to promote developmental biology research and at the same time led the Committee of Developmental Biology to collect statistical records of research topics and personnel in American development biology (Brauckmann, 2004; Report of the National Academy of Sciences, 1954, pp. 50–51). In the Annual Report of the Division of Biology and Agriculture for 1953–1954, Weiss reported that the Committee on Developmental Biology had reviewed and classified 15,600 research projects from the Bio-Sciences Information Exchange, and found that 1,090 (around 7%) had "some bearing on developmental biology." Moreover, "it was noted that while certain lines of attack are greatly favored other basic problems are seriously neglected; for instance, Developmental Patterns (total of 7 projects); Cell Migration (8 projects); etc." (Annual Report of Activities of the Division of Biology and Agriculture for the year July 1, 1953 to June 30, 1954, p. 16). The records of the Committee's survey do not survive, but these reports reveal that Weiss was seeking a systematic understanding of research in the United States and that the results of that survey justified his concern that areas of what he referred to as developmental biology were being neglected. Weiss believed that conceiving of the study of development in terms of 'developmental biology' would promote a more integrated study of development where important areas of research could not be neglected as easily.

To champion his interest in promoting the field even further, when Weiss was chairman of the Division of Biological and Agriculture (DBA) for the National Research Council (NRC) he pushed the term 'developmental biology' as a funding category to rival competing groups such as 'molecular biology,' 'genetic biology,' and 'cellular biology,' which he also singled out as separate funding designations (Appel, 2000, p. 63). Weiss' funding designations eliminated the traditional classification system of biology that relied on organism (botany, zoology, microbiology, etc.) and instead focused on the level of functional analysis. The new National Science Foundation adopted a variation of Weiss' scheme in 1952 when it reorganized its biological funding policies (Appel, 2000, p. 63). This realignment was motivated by a concern that "biology was becoming more and more splintered" (Appel, 2000, p. 67). During the early 1950s, Weiss attempted to use his power as chairman to create a more unified direction for biology in the United States that integrated the various disciplines in ways that they had not been

⁵ For a broader discussion about naming conventions in the formation of disciplines, see Powell, O'Malley, Muller-Wille, Calvert, & Dupre, 2007.

previously. Ultimately, Weiss' plans for using his position at the NRC to achieve a unified biology funding policy were thwarted by NSF leaders, who thought Weiss' group at the NRC duplicated too much of the NSF's efforts (Appel, 2000, pp. 121–27). Weiss failed at managing the federal funding for biology in the United States, but his functional grouping of biological disciplines would live on, and the term 'developmental biology' would become widely adopted by societies throughout the world.⁶

Though Weiss' label became the common nomenclature for the discipline throughout the world, we can't assume that each national society adopted the terminology due to national funding priorities similar to those found in the United States' political scene. Instead, it is more likely that the term 'developmental biology' captured a change in the discipline with which individual organizations (from international societies to university departments) and scientists identified. For some, the previous label of 'embryology' designated an outmoded form of analysis. Tokindo Okada recalls that "many Japanese considered that 'Embryology' was already an old-fashioned term [by the 1950s], since it denotes only the morphological description of normal development." Okada remembers that "they preferred to call the new science of development 'Experimental Embryology and Experimental Morphology,'" though that had a lot to do with the fact that many Japanese biologists had been trained in the German tradition of *Entwicklungsmechanik* (Okada, 1994, p. 137).

One aspect of all of the historical interpretations of this period is that they relied on a narrowly focused set of data to make their claims. Horder and Weindling rely on an analysis of the topics discussed at the United States-based annual Growth Symposia from the late 1930s through the 1950s. Nick Hopwood, as well as the authors writing in the special issue edited by Burian and Thieffry, rely on historical case studies of some of the most prominent researchers in the field. Brown and Oppenheimer draw extensively from personal experiences for their perspectives. What would be helpful in adjudicating among these theories about the post-World War II change from embryology to developmental biology is a much larger set of data that is neither restricted by nationality nor focused on specific individuals.⁷ If we want to articulate what was going on throughout the field, we need to look at as much development-focused research as possible during this period in order to develop descriptions of this transition that actually encapsulate the field itself. Thus, we have extracted the data within the *GEIS* to see what types of trends and themes that we can associate with this change.

3. Documenting diversification: the General Embryological Information Service

The Hubrecht Laboratory in The Netherlands first published the *General Embryological Information Service (GEIS)* in 1949 to foster international collaboration and disseminate information about current work in the field of embryology. By collecting statistics from embryologists about their current research and then organizing it for easy dissemination, the publishers hoped that the *GEIS* would help rebuild the relationships of a scientific community that had been fractured during World War Two, a goal that echoed the ideals

associated with the establishment of the Hubrecht Laboratory in the aftermath of World War One.

In 1916, the Royal Netherlands Academy of Sciences had founded an international institute to honor the memory of one of their country's most respected biologists, Ambrosius Arnold Willem Hubrecht (1853–1915). Hubrecht had been a prominent comparative embryologist and defender of Darwin in the late nineteenth century. In the last years of his life, Hubrecht had focused on building international collaborations between embryologists in Europe, founding the *Institut International d'Embryologie* (IIE) in 1911 to help facilitate this goal.⁸ Unfortunately, along with Hubrecht's death in 1915, the onset of World War One significantly affected international collaboration among embryologists, and scientists in general. However, Hubrecht had amassed a prestigious scientific reputation and an impressive comparative embryology collection, two things that the Royal Netherlands Academy did not want to let go to waste (Faase, Faber, & Narraway, 1999).

The Dutch, who officially remained neutral during the hostilities, wanted to preserve a semblance of international collaboration after the war and founded the Hubrecht Laboratory in 1916 with the specific mission of fostering international scientific collaboration. The Royal Netherlands Academy of Sciences appointed Daniel de Lange the first director. De Lange kept the international focus of the laboratory intact for the next thirty years, allowing the immense collection of embryological material to be available to any interested researchers. De Lange continued to enhance the collection during his tenure, but the majority of the materials came from Hubrecht himself (Faase et al., 1999).

It should be noted that this early history of the Hubrecht Laboratory illustrates how embryology during the first half of the twentieth century is more complicated than the traditional historiography of late nineteenth and early twentieth embryology. The standard narrative has been that the end of the nineteenth century marked the rise of experimental embryology (and experimental biology, in general), at the expense of comparative and descriptive embryology (Allen, 1978). In particular, historians have pointed towards the experimental work of Hans Driesch, Wilhelm Roux, and the rise of *Entwicklungsmechanik* that began in the late nineteenth century and led to Hans Spemann's work on induction and the organizer, for which he won a Nobel Prize in 1935. Recent scholarship, however, has shown that this interpretation of embryology's trajectory is too simple (Hopwood, 2009). The classical narrative creates the impression that embryology left comparative and descriptive work behind to concentrate on the motivating questions and techniques of experimental embryology. As Nick Hopwood (2009) shows, this depiction not only over privileges experimental embryology, making it appear to be the only type of research occurring at this time, but obscures the diversity of work that took place during this period. The founding of the Hubrecht Laboratory justifies this more nuanced narrative; Hubrecht's *Institut International d'Embryologie* was the first international embryology organization, which notably focused on descriptive and comparative work rather than experimental work that supposedly dominated the field at that time. Hopwood also points out that important embryological work took place in other areas beyond traditional zoology departments. In particular,

⁶ Weiss also played a role in the creation of the Society of Cell Biology in the United States, showing again the leadership role that Weiss played in the reorganization of biology as a whole during this period. Paul Weiss to Morgan Harris, March 20, 1959. Rockefeller Archive Center, RG 450 W436: Paul A. Weiss Collection, Series 2, Box 6, Folder: American Society for Cell Biology.

⁷ Our emphasis on trying to use *GEIS* data to articulate larger trends in the field contributes to the recent discussions regarding big data in history. See Grossman, 2012 and Ewing et al., 2014.

⁸ The *Institut International d'Embryologie* has an interesting history. At first, it had a very limited and selective membership. It held sporadic meetings in the interwar period and eventually became a part of UNESCO after World War II, which the Hubrecht Laboratory also became associated with during that time. The IIE would eventually loosen its membership requirements in the 1950s, and in 1968 would change its name to the International Society of Developmental Biologists. For more information see Faase et al., 1999; Slack, 2000; Palmeirim & Aréchaga, 2009.

embryology was important in medical schools and also had a place in botany departments (Hopwood, 2009).

In 1947, the Royal Netherlands Academy of Sciences appointed a new director of the Hubrecht Laboratory, who changed the direction of the institute. The new director, Chris P. Raven, was an embryologist in the experimental tradition, having been trained under Martinus W. Woerdeman, a student of Hans Spemann (Woerdeman & Raven, 1946). At the time of his appointment, Raven also acted as the head of the Zoological Laboratory Facility of Science at the University of Utrecht (GEIS, 1949, p. 56). To help keep the Hubrecht Laboratory running at peak efficiency, Raven's student Pieter D. Nieuwkoop was hired as the deputy director in charge of daily management (Faase et al., 1999, p. 586).

Together Raven and Nieuwkoop quickly developed an expanded vision of the Hubrecht Laboratory that went beyond simply providing the international community access to a comparative embryological collection (Gerhart, 1997). In 1948, Nieuwkoop sent a survey to a large number of departments, institutes, and researchers studying any aspect of embryology at the time, intending to gather information on researchers and their current projects. Besides asking for their address and qualifications, the survey also inquired about their current unpublished work (GEIS, 1949, p. 5–7). After receiving feedback, the Hubrecht Laboratory published the findings of the 550 people who responded in the *General Embryological Information Service* in 1949. Nieuwkoop envisioned the report as a resource for researchers interested in finding others conducting similar work, for determining where the field was heading, and for providing contact information. They specifically wanted to collect data on ongoing projects, rather than published works, since bibliography services already existed (GEIS, 1950, p. 5). They imagined that reports of current work produced richer information about the research going on throughout the discipline and provided more opportunities for researchers to see where duplicative efforts were occurring, rather than finding out only after something was published.

After the first publication of the *GEIS*, the Hubrecht Laboratory received overwhelming support to continue the service (GEIS, 1950, p. 5). Nieuwkoop continued building the network of contacts, which at first had a strong European focus. Soon, however, the *GEIS* featured the majority of embryologists from North America, Europe, Asia and areas even more distant including South American, Asian, Pacific, and African countries. By the early 1970s the *GEIS* was publishing data on nearly 3000 scientists working in fields studying growth and development (GEIS, 1971, p. 5). Nieuwkoop would take over the directorship of the Hubrecht laboratory in 1953, and stayed in the position till he retired in 1980 (Gerhart, 1997).

Each issue of the *General Embryological Information Service* contained a considerable amount of information. Just as the *Drosophila Information Service* had done yearly since 1934 for *Drosophila* research, *GEIS* included a directory of all the embryological laboratories and their researchers.⁹ The directory was broken down in two ways: geographically and alphabetically. The geographic list contained a catalog of institutions and employees by continent, country, state, city, and institution. The alphabetical list included more than just relevant addresses; it also listed their current areas of research. For some, the listing might include several different ongoing project titles. For others it may only list one or two subjects. Often the list also indicated, intentionally or

not, the gender of the researcher by using the descriptor Ms. or Mrs. in front of their names.

The *GEIS* editors also created a subject directory based on the reported research topics.¹⁰ This research index allowed those interested in a particular topic to find out who else was working in that area. For instance, if someone in 1959 wanted to see who else was working on issues related to hormones and metamorphosis, he or she could look under the broad division of “VII. Metamorphosis” and then the subdivision “b. hormones and metamorphosis” (see Fig. 1). There, one could find a list of the researchers who reported research in that area.

Following an experimental tradition stemming from Spemann's laboratory, research at the Hubrecht Laboratory after the war concentrated on studies of induction in amphibians, frogs, and fowl. Nieuwkoop's lab worked on projects that they classified in the *GEIS* as research in Experimental Developmental Morphology, specifically cataloging it under the topic Further Development of Chordata, and subtopics of Induction, Determination, etc. (II.7.c.) and Development of Organ Systems and Organs, Central Nervous System (II.7.e.). The *GEIS* research classification reached well beyond the Hubrecht laboratory's areas of interest, however, to try to encompass a very broad range of work on development and growth.

The *GEIS* research subject index changed in response to changes in the field. The editors revised their research subject index on several occasions from 1949 through 1963. In the second issue (1950), the editors combined “Comparative Embryology” and “Descriptive Embryology,” two of the largest divisions and restructured some of the subcategories. Another major revision occurred in 1961 when the editors sought to restructure many of the divisions to “render the system more logical, more up-to-date and easier to use” (GEIS, 1961, p. 5). By 1965, the editors decided that the system needed to be dramatically reorganized and created an alphabetical list of topics, removing the larger divisions such as “Descriptive and Comparative,” “Experimental Developmental Morphology,” “Developmental Physiology,” and “Development and Genetics”. The previous systematic method of organization, the editors said, “was sometimes difficult to fit work carried out with modern methods into the system in such a way that it could be easily retrieved” (GEIS, 1965, p. 5).

The alphabetical subject index, along with the usual directory of researchers and institutions, continued until the *GEIS* folded in 1981. With the diversification of professional societies, more specialized journals, and increased communication throughout the world, the Hubrecht Laboratory had to discontinue their service because of decreased subscriptions. The *GEIS* had, however, by that point accomplished the original goals of Raven and Nieuwkoop. The service had kept the Hubrecht Laboratory relevant, fostered international collaboration after World War Two, and effectively disseminated information throughout the global community. By 1980, researchers had many outlets for collaboration and information, making the *GEIS* obsolete, particularly considering the significant amount of administrative work that went into collecting and compiling the information.

4. Measuring diversification

Just as the new historiography of the nineteenth and early twentieth century argues for a more heterogeneous picture of

⁹ For a discussion of *Drosophila Information Service* (*DIS*) see Dietrich & Tambarco, 2007. The most significant difference between the *DIS* and the *GEIS* was the latter's inclusion of a subject index, which was needed considering the exponentially larger number of questions, methods, and areas of research that fit under the rubric ‘embryology’ versus just those scientists that worked on *Drosophila*.

¹⁰ How exactly the *GEIS* editors created the subject directory is unclear. Given some of the language in the introductions to the early *GEIS* volumes, it seems that the editors asked scientists to simply report their research and the editorial staff categorized the reported research as they saw fit (the work was said to be mostly done by Nieuwkoop).

VI. 3d

Endocrine glands

Belka, A. — a
Chachulska, W. — a

VII. 2b

Pluta, E. — a, b
Heckerman, R. O. — b L
Wróblewski, R. — a M

VII. METAMORPHOSIS

SUBDIVISION

- 1 *Theoretical problems and general questions*
 - 2 *General investigations*
 - a General subjects
 - b Hormones and metamorphosis
 - c Metamorphosis of part of the organism
 - d Metamorphosis of special organ systems
- (Cf. general subdivision p. 173–175)

CHARACTER OF INVESTIGATION

(5) Chemical treatment

- | | | |
|---|--------------------|------|
| 1 <i>Theoretical problems and general questions</i> | Niizima, M. — a | J |
| | O'Steen, W. K. — b | J |
| | Stuchly, Z. — a | J |
| 2 <i>General investigations</i> | Urbani, E. — a | J |
| a General subjects | Yanagisawa, T. — a | (1)J |
| Hauenschild, C. — a | C | |
| Bookhout, C. G. — b, c | D | |
| Bückmann, D. — a | D | |
| Egelhaaf, A. — b | D | |
| Gloor, H. J. — a | D | |
| Hadorn, E. — d | D | |
| Harada, M. — a | D | |
| Ito, T. — a | (1)D | |
| Laufer, H. — b | D | |
| Piepho, H. — a | D | |
| Pohley, H. J. — a, b | D | |
| Rockstein, M. — a, b | D | |
| Ulrich, H. — b | D | |
| Urbani, E. — a | D | |
| Ursprung, H. — a | D | |
| Lynch, W. F. — a | (5)F | |
| Harvey, Mrs. E. B. — c | G | |
| Brewin, B. I. — a | H | |
| Lynch, W. F. — a | (5)H | |
| Baxter, E. W. — a | I | |
| Castigli (Pitotti), Mrs. M. — b | J | |
| Dent, J. N. — b | J | |
| Fankhauser, G. — d | J | |
| Kiortsis, V. — c | J | |
| Nonaka, T. — a | J | |
| b Hormones and metamorphosis | | |
| Banarjee, M., Ganguly, D. N., | | |
| Sarkar, D. N., Banarjee, P., | | |
| Dev, D. and Bose, B. — a | D | |
| Bodenstein, D. — d | D | |
| Geigy, R. — a | D | |
| Highnam, K. C. — a | D | |
| Ichikawa, M. and | | |
| Nishiitsutsuji (Uwo), | | |
| Mrs. J. — a | D | |
| Novák, V. J. A. — a | D | |
| Piepho, H. — a | D | |
| Nowakówna, Miss J. — a | V | |
| Radecka, Mrs. E. | | |
| Erdman — a | V | |
| Sembrat, K. — c | V | |
| Wurmbach, H. — a | V | |
| Iwasawa, H. — a | I | |
| Iwasawa, H. — a | J | |
| Fraser, R. C. — b | J | |
| Gawronówna, Miss M. — a | J | |
| Kaltenbach, Mrs. J. C. — b, c | J | |
| Kollros, J. J. — b, f | J | |
| Lynn, W. G. — a | J | |

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Fig. 1. Sample Page of *GEIS* Research Classification, Metamorphosis 1959. The *GEIS* contained three types of directories: Alphabetical, Geographical, and Research Classification. This page is the first Research Classification page for the research area of Metamorphosis in 1959. Note that the system of research topics is given and then individual research projects are listed by author's last name, first initial, and then a dash followed by a lower case letter indicating the specific project. Upper case letters on the right of each column indicate the organism used in that research project.

embryological work, the historical patterns evident in *GEIS* records point to the growing diversity of projects and people associated with terms “embryology” and later “developmental biology.” The *GEIS* directories offer a global index of developmental biologists and

their work during the crucial period before and during developmental biology's naming. In particular, their classification of each research project by major research areas and then by topics within each area allows historians to create an overview of different

research areas and how they changed over time. We realize that the *GEIS* classification system reflects the views of Raven, Nieuwkoop and their staff, but these actors' categories still offer a valuable lens through which to view global patterns of research. Moreover, because we can follow how the system of classification evolved and the popularity of research topics and areas changed over time, we can describe how research on development grew and diversified from 1950 to 1963.

To make use of the rich resource of the *GEIS* surveys, we compiled a series of spreadsheets with data on researcher names and research projects, as well as the classification of those projects according to the *GEIS* schemas. From these spreadsheets, we tallied simple quantitative measures of the number of researchers per year and the change in the number of research projects in a particular research topic.¹¹ However, we wanted to adapt more complex quantitative tools to this dataset, while finding appropriate ways to describe and visualize the many relationships that are embedded in the data we had extracted.¹²

In order to describe research diversity in the *GEIS* research classification, we developed an analogy with the way that ecologists measure species diversity. Ecologists distinguish between species richness and species diversity by using species richness to describe the total number of different species within a given area at a particular time and species diversity to describe the distribution of organisms within those species. We drew an analogy between the geographic area used by ecologists and a research area categorized by the *GEIS*. In other words, within a research area used in the *GEIS* classification, such as Developmental Genetics, research topics, such as "Phenocopies" or "Lethal Factors," were thought of as analogous to individual species. We measured research topic richness by counting the number of research topics in each research area per year. The results are represented graphically in Fig. 2a.

Topic richness alone is not sufficient to capture diversity in the environment, however. Ecologists realized that the distribution of organisms across species was an important consideration in measurements of diversity. Two geographical areas could each have twenty different resident species, for instance. So, their species richness would be identical, but in one area 90% of the organisms could be members of a single species, while in the second area the species could be more evenly distributed among the twenty species. In this case, we would want to say that the more evenly distributed scenario represents more species diversity than the scenario where the overwhelming majority of individuals are members of a single species. Applying this thinking to developmental biology research, in order to measure research diversity, we need to measure the distribution of research projects across research topics in a given research area in a given year. Having compiled the relevant data into spreadsheets, we adapted the Simpson Diversity Index from ecology and biodiversity studies to calculate the research diversity per research area in a given year (Simpson, 1949).¹³

Simpson's diversity index is calculated from the distribution of reported projects across research topics using the following equation:

$$D_s = 1 - [(\sum n_i(n_i - 1)) / (N(N - 1))] \quad (1)$$

In this equation, "N" is the total number of reported projects within all research topics in the research area and " n_i " is the number of individual reported projects within research topic "i". The value of D_s ranges from 0 to 1 and can be interpreted as the probability of randomly picking two research projects from different research topics within a given area. Higher values of D_s reflect higher diversity. The D_s measure is dependent on both the number of topics and the evenness of the distribution of reported projects in each topic. Overall, diversity is minimized when all of the research projects belong to a single research topic, and diversity is maximized when each research topic has an equal number of research projects. The more evenly distributed projects are among topics, the higher the diversity index will be.¹⁴

Measures of topic richness (R) and diversity (D_s) for data from the *GEIS* reveal a significant transition between 1959 and 1961 (See Fig. 2a and b). At this time, topic richness (R) in developmental physiology declines, while topic richness in descriptive and comparative embryology, developmental genetics, development and pathology, regeneration, and metamorphosis increases. The topic diversity (D_s) increases in every topic area between 1959 and 1961, although the increase is much greater in areas such as metamorphosis and developmental genetics. The shift in both topic richness and diversity in this interval means that the *GEIS* editors changed their research classification to include more topics and then distributed research projects more evenly across those projects in 1961 when compared to the distribution across topics in 1959. While the change in the *GEIS* occurred between 1959 and 1961, this does not mean that developmental biology itself underwent a significant change just between 1959 and 1961. Rather, changes in the field had probably been building for a number of years, and in 1960, Nieuwkoop and the *GEIS* editors decided to implement a significant revision of their classification system.

While quantitative measures of topic richness and topic diversity indicate that important changes occurred between 1959 and 1961, they do not provide much information about the nature of that change. In order to gain a better understanding of how the *GEIS* research classification and distribution of research projects changed between 1959 and 1961, we traced the classification of all of the research projects from 1959 to 1961 (3,366 total projects) by area and topic.¹⁵ Using category analysis in the program Parallel Sets, we then visualized the pattern of change in research classification from 1959 to 1961 (see Fig. 3) (Parallel Sets, Kosara, Bendix, & Hauser, 2006). This software tracks individual entries across multiple categories and then produces a dynamic visual representation of the categorization. Because we are interested in the change in how these projects were represented within research areas and how the research area and topic assignments changed from 1959 to 1961, we used Parallel Sets to track the trajectories of all of the research projects across both research areas and topics. Fig. 3 represents the trajectories of the 3,366 projects across the research areas listed in 1959 and 1961. Projects represented in the 1959 classification, but not in 1961, are listed as "Projects Ending between 1959 and 1961," whereas projects found in the 1961 but not 1959 are classified as "New Projects in 1961." The bands linking the research topics in Fig. 3 represent the trajectories and relative proportions of how many individual research projects were listed under each area in 1959 and 1961. Given the change in richness and

¹¹ These spreadsheets are available at the HPS Repository. See "GEIS Research Topics Data, 1959–1961" go to <https://hpsrepository.asu.edu/handle/10776/8287> (accessed April 9, 2015).

¹² This is a part of a larger trend in HPS that is occurring at the moment, which is sometimes referred to as digital or computational HPS (Laubichler, Maienschein, & Renn, 2013).

¹³ These spreadsheets are available at the HPS Repository. See "Growth in GEIS Research Areas, 1949–1963" go to <https://hpsrepository.asu.edu/handle/10776/8288> (accessed April 9, 2015).

¹⁴ A similar quantitative approach to journal biodiversity is taken in Dietrich, Ankeny, & Chen, 2014.

¹⁵ These spreadsheets are available at the HPS Repository. See "Research Diversity and Richness in GEIS, 1950–1963" go to <https://hpsrepository.asu.edu/handle/10776/8289> (accessed April 9, 2015).

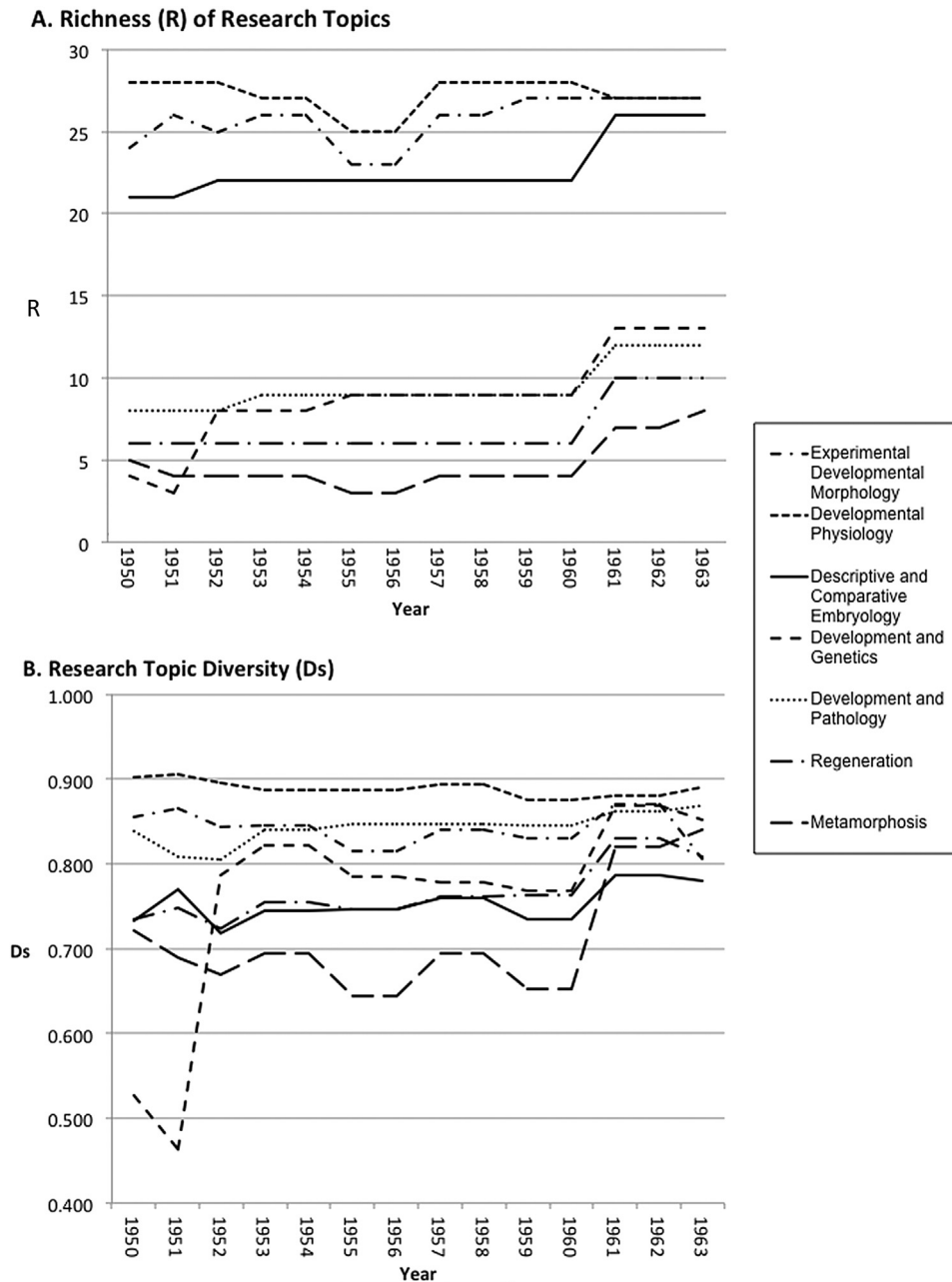


Fig. 2. Research Richness and Diversity for Developmental Biology, 1950–1963. (a.) Topic richness measures the number of research topics listed in the *GEIS* research classification for a given year. The rise in topic richness between 1959 and 1961 reflects a significant addition of new research topics to the classification system. (b.) Topic diversity was calculated using Simpson's Diversity Index for each research area. Diversity represents the distribution of research projects among the research topics available for that research area for a given year. The rise in diversity between 1959 and 1961 reflects a more even distribution of research projects among research topics than in previous years.

diversity between 1959 and 1961, we expected to see significant reclassification of projects. We were surprised, however, by how many projects began and ended during this time period. 28% of the projects classified in 1961 were new. This means that the changes in topic diversity cannot be ascribed only to reclassification by the *GEIS* editors.¹⁶ Instead, the birth and death of projects in each area must be considered as important sources of change as well.

In order to get at more fine-grained changes within a research area, we extended the same kind of categorical analysis using Parallel Sets to the trajectories of research projects between research topics within a research area. For instance, Fig. 4 depicts the trajectories of projects within the research area “Development and Pathology.” Although the Diversity Index for this research area is almost unchanged between 1959 and 1961, the combined trajectories of individual research projects in this area reveal a tremendous amount of change, including a very large proportion of new projects in 1961. The Diversity Index reflects only the distribution of projects across topics in a particular year. Thus, without looking closely at the Parallel Sets analysis, it would be impossible to see all of the types of changes that occurred in this area.

¹⁶ We did not conduct any tests of statistical significance with our data. We know that errors of classification are a part of the *GEIS*, and we are sure that there have been errors in our counting and recording of data. Accordingly, we take our results with a grain of salt, and use them as indicators of general trends that can be trusted more when the differences are greatest.

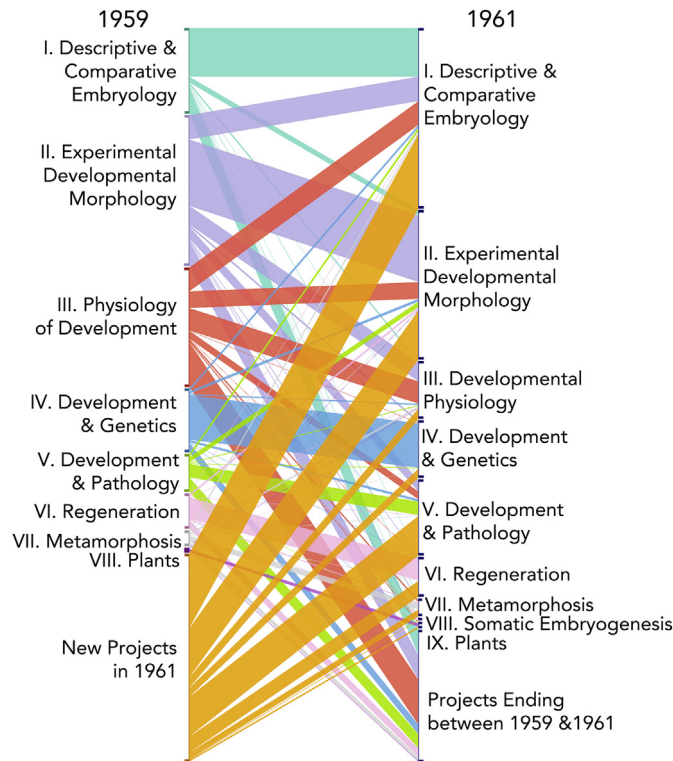


Fig. 3. Change in the Classification of Developmental Biology Research Areas between 1959 and 1961. Using Parallel Sets software, this figure represents the trajectories of 3,366 research projects from *GEIS* research areas listed in 1959 and to those in 1961. The width of each band corresponds to the number of individual research projects in that particular trajectory. Projects from 1959 could either remain in the same research area, be reclassified into another research area, or end before 1961. New projects in 1961 are also represented in this diagram.

Visualizing project trajectories reveals a more complex dynamic process that is not captured by diversity and richness measures alone. An individual research project can follow five possible trajectories between the research classifications for any given two time periods: 1) a research project can remain classified in the same research topic or area; 2) a research project from 1959 can end; 3) a research project can begin in 1961; 4) a research project can be reclassified to a new topic within the same research area; or 5) a research project can be reclassified to a new topic in a new area. When we quantify the contributions of these kinds of changes within a research area (see

Table 1), we find that only regeneration and developmental genetics have more than 50% of their projects continuing within the same research area. The other research areas have higher rates of reclassification or movement from one area to another. Development and Pathology has the lowest proportion of continuing projects at 18% and the highest proportion of new projects at 52%.

The challenge presented by these patterns of change lies in understanding their underlying causes, whether the pattern represents topic richness, topic diversity, or the trajectories of research projects. We appreciate that no simple explanation is going to do justice to the complex global dynamics represented in the *GEIS* data, but we are confident that the patterns we have discovered can lead to some representative cases that will shed light on the changes that contributed to the diversification of research in embryology and developmental biology.

5. Illustrations of diversification: the case of nuclear transplantation

The research area “Development and Genetics” offers an interesting example of how research projects proliferate, migrate, and die in our focused time frame. Overall, the “Development and Genetics” research area increased in size between 1959 and 1961, going from 179 to 243 reported projects (see Fig. 5). Similarly, the number of topics increased as well, going from nine topics in 1959 to thirteen in 1961. Whether or not the growth in the total number of topics drove the *GEIS* editors to diversify the topics is unclear. However, what is clear is that the editors did not create new topics in order to place only a few reported projects within them. Rather, a healthy number of projects migrated from where they were previously listed in 1959 into the new 1961 topics. In other words, *GEIS* editors created the new headings for a critical mass of projects that warranted their own topic.

One of the newly created topics in 1961 was “nuclear transplantation studies.” It is not the case that scientists had just developed nuclear transplantation techniques in the intervening year between the 1959 and 1961 *GEIS* indexes. Rather, nearly a decade before, in 1952, Robert Briggs and Thomas King had published the first paper articulating the successful use of the procedure. Since that publication, Briggs and King had continued to carry out nuclear transplantation studies in their laboratory at Lankenau Hospital Research Institute in Philadelphia, training postdocs and visiting scientists throughout the period (Crowe, 2014). Several of the people associated with their laboratory during the 1950s appeared in the new nuclear transplantation

Table 1
Changes in developmental biology research from 1959 to 1961.

Research area	Number of research projects per area in 1961	Continuing projects (As a proportion of total in research area in 1961)	Projects reclassified from other areas (As a proportion of total in research area in 1961)	New projects (As a proportion of total in research area in 1961)	Projects ending before 1961 (As a proportion of total in research area in 1959)
I. Descriptive and comparative embryology	852	27%	32%	41%	30%
II. Experimental developmental morphology	705	44%	23%	33%	16%
III. Developmental physiology	273	38%	44%	18%	38%
IV. Development and genetics	271	77%	7%	16%	15%
V. Development and pathology	360	18%	30%	52%	37%
VI. Regeneration	188	54%	7%	39%	24%
VII. Metamorphosis	84	32%	30%	38%	27%
VIII. Somatic embryogenesis	13	0	77%	23%	n/a
IX. Experimental developmental morphology of plants	31	48%	27%	25%	14%

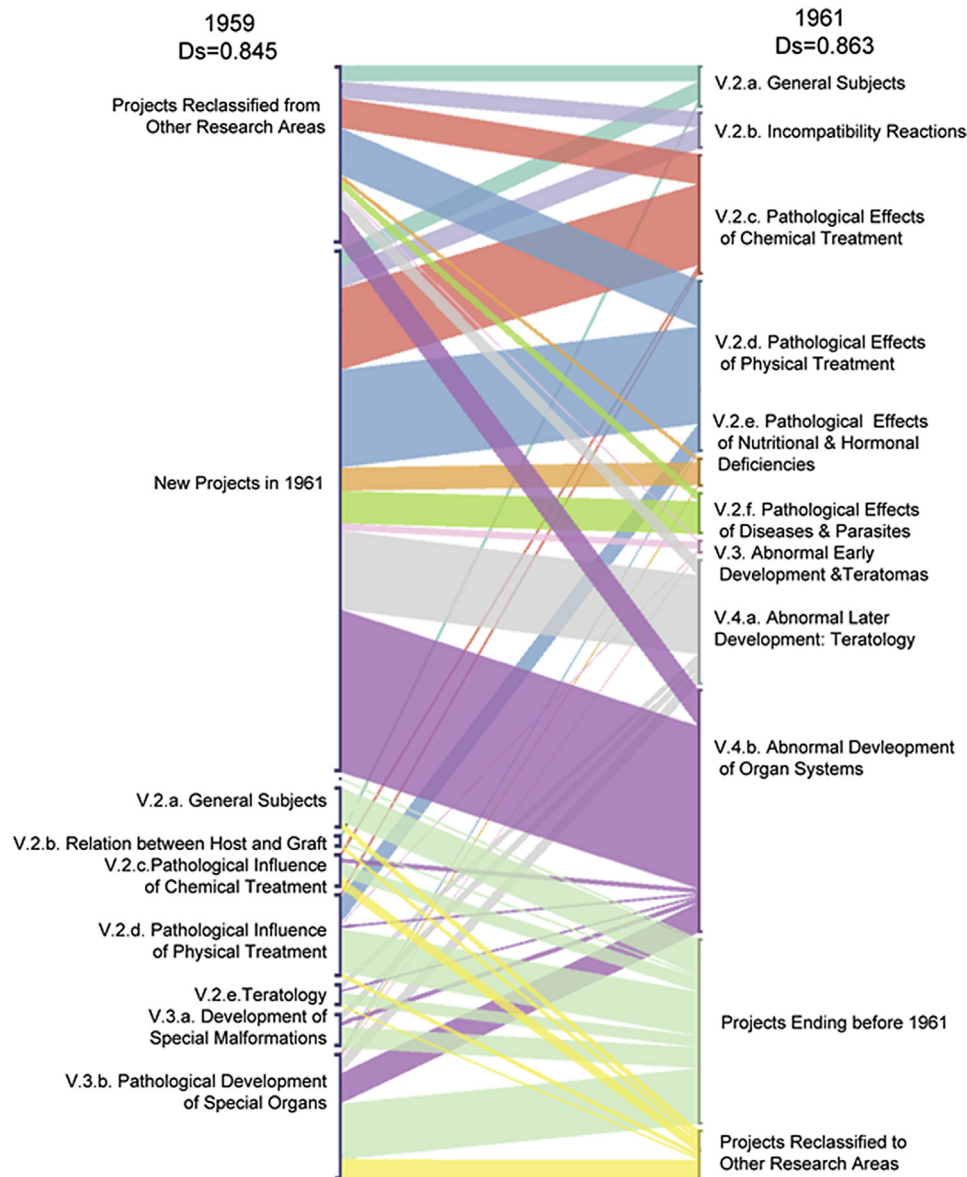


Fig. 4. Change in the Classification of Research Projects within the Development and Pathology Research Area between 1959 and 1961. Using Parallel Sets software, the figure depicts the trajectories of research projects within Development and Pathology. The width of each band corresponds to the number of individual research projects in that particular trajectory. Even though the Diversity Index changes only slightly between 1959 and 1961, the change in classification and project distribution is extensive.

subheading in 1961, including Marie DiBerardino, Robert McKinnell, and Steve Subtelny. However, by the end of the 1950s several laboratories not associated with the research program initiated by Briggs in Philadelphia had also taken up the technique. In 1961, enough researchers throughout the world had reported working with the technique to convince *GEIS* editors to create a separate category for their work. For instance, the other scientists who reported doing nuclear transplantation studies in 1961 included John Moore at Columbia University, two scientists working in Czechoslovakia at Charles University, and two working in the USSR in the Institute for Animal Morphology (*GEIS*, 1961, p. 239).

Out of the ten listed projects in the new area in 1961, only two of the projects had not been listed in 1959. In earlier volumes, *GEIS* editors had listed nuclear transplantation projects within a variety of other topics. The nuclear transplantation studies of Briggs and King had first been listed in 1952 under the “General

Subjects” heading of “Initial Development” within the “Experimental Developmental Morphology” research area (*GEIS*, 1952, p. 132).¹⁷ By 1959, Briggs and King’s nuclear transplantation studies were listed in several places within the Experimental Developmental Morphology research area, including “Further Development of Vertebrates, Histo- and cytogenesis,” and “Growth and Differentiation, b. Differentiation.” *GEIS* editors also began listing their work within the “General Subjects” heading of the “Development and Genetics” research area (*GEIS*, 1959, p. 208). By 1959, most of the nuclear transplantation work being reported by scientists such as Michael Fischberg and Tom Elsdale at Oxford University, whose lab future Nobel Prize winner John Gurdon would enter in 1957, was also classified within the “general

¹⁷ Briggs and King’s work was also listed under ‘Differentiation’ sub category (II.8.b.) of Experimental Developmental Morphology. *GEIS*, 1952: 137.

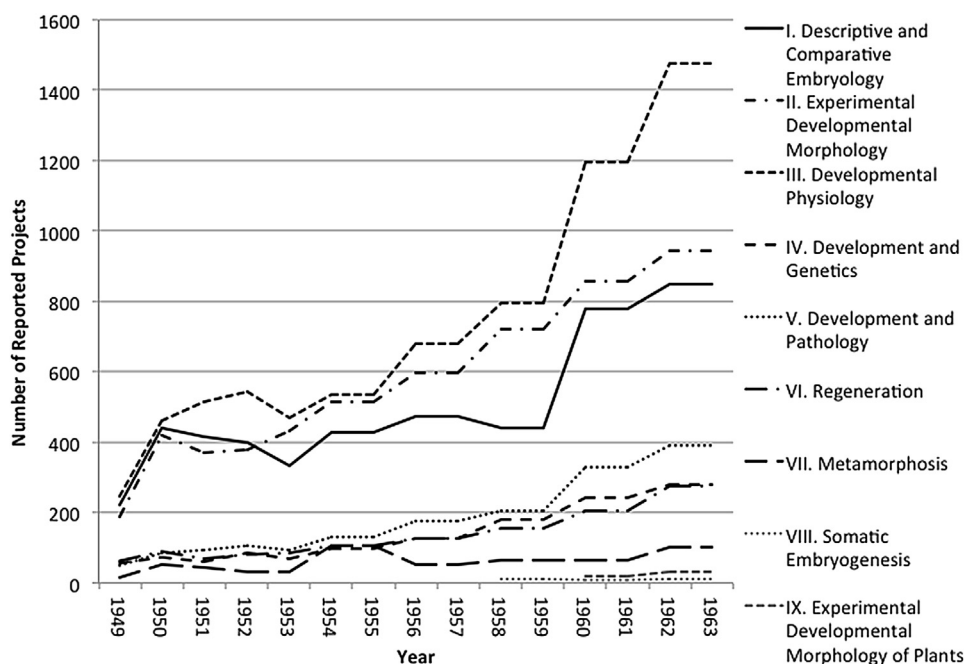


Fig. 5. Growth in GEIS Research Areas, 1949–1963. The total number of research projects listed per research area per year. Note significant growth in Descriptive and Comparative Embryology, Experimental Developmental Morphology, Developmental Physiology, and Development and Pathology in the period between 1959 and 1961.

subjects” topic of the Development and Genetics research area (*GEIS* 1959, p. 208).¹⁸

By the time that *GEIS* editors created the nuclear transplantation studies category in 1961, some scientists had already abandoned work in the area. For instance, G.V. Lopashov at the Institute of Animal Morphology in the Soviet Union had reported doing work with the technique in 1959, which the *GEIS* categorized under “Merogony” in the “Development and Genetics” research area (*GEIS*, 1959, p. 209). In 1961, Lopashov had dropped the technique from his list of ongoing projects (of which there were four in 1959 and three in 1961). Similarly, a laboratory at Charles University in Prague led by F. Sládeček had been working on nuclear transplantation research for a number of years and listed new assistants each year. Thus, A. Romanovsky and J. Nedvidek reported nuclear transplantation projects in 1959, which were listed in similar fields as Briggs and King’s work, but were not listed in 1961 as those particular scientists had moved on to different projects.

The *GEIS* classification of nuclear transplantation projects in 1959 and 1961 is a good example of how useful this research index is for historians. For our thesis, the creation of the nuclear transplantation studies heading shows how the larger field of developmental biology diversified and grew in the late 1950s and early 1960s. The creation of a nuclear transplantation studies category in 1961 was a recognition of the technique as an important area of research conducted by biologists from around the world, not just by one or two select people. Previously the *GEIS* editors had scattered the work into several different areas, but as the number of nuclear transplantation studies researchers grew it became apparent that a new category was needed. After all, the *GEIS* was created to help researchers find who was doing similar work and if nuclear

transplantation studies were dispersed across a number of topic areas than it would be difficult to create the type of collaborations that the Hubrecht Laboratory administrators hoped to foster.

By mandating that the *GEIS* reflect what scientists were actually working on in the laboratory, not just bibliographic information of recent articles, the editors have also given historians a glimpse into how fluid the field surrounding development and growth was during this period. For instance, the history of nuclear transplantation has primarily focused on the work of Briggs and King in the 1950s and the later work of John Gurdon at Oxford in the early 1960s. Though both of these laboratories appear in the *GEIS*, so too do several other researchers who have never entered into the published histories of the technique. Several of these scientists never published any work concerning nuclear transplantation, but the *GEIS* data shows that the technique was being employed (or at least attempted) in several laboratories around the world, not just in the Anglo-American context. Researchers in these labs might have picked up the technique in an attempt to apply it to their own work, or perhaps they were inspired to ask similar questions to Briggs, King, and Gurdon. For any number of reasons the researchers abandoned the technique in favor of other investigations, never leaving a publication to document their efforts. With *GEIS*, historians can get a better picture of how fluid laboratory work was in many places. Many of our histories focus on the creation of important research traditions by well-known scientists. In contrast, *GEIS* shows how the rank-and-file biologists in developmental biology often took up new techniques only to discard them later, how they dabbled with different organisms without ever publishing material using them, and, in general, carried out very ordinary investigations that did not produce a multitude of publications nor drive research into a completely new direction.

More broadly, by tracking the number of researchers included in the index and the increasing number of topics from the late 1940s into the 1960s, historians can see how the discipline at large changed during this period. Rather than an expansion of one particular area, *GEIS* editors reorganized the index in order to make room for new topics that had garnered a critical mass of

¹⁸ Fischberg, Elsdale, and Gurdon’s work was not be listed in the 1961 *GEIS*, though their names were listed in the directory. We assume that this is simply because they did not fill out a survey for that year, which is not surprising given that this is the period in which Fischberg moved to the University of Geneva and Gurdon was finishing a postdoc in California. Gurdon would later take Fischberg’s vacant position at Oxford.

investigators. Thus, the diversification and richness of the topics throughout the history of *GEIS* reflects how the field did not restrict itself to a select few topics, but rather continued to expand the types of questions, methods, and theories that were included under the rubric of 'general embryology,' or as many societies came to call it—'developmental biology'.

6. The molecularization of developmental biology

According to a number of historians, one of the major differentiating factors between embryology and developmental biology was the influence of molecularization and molecular biology, or, more specifically, the incorporation of analysis and data from the molecular level (Burian & Thieffry, 2000; de Chadarevian, 2000; Fantini, 2000a, 2000b, 2000c; Morange, 2000a). Fortunately, in 1961, the editors of *GEIS* included two systems of classification that shed some light on the molecularization of development.

In 1957, 1959, and 1961, the *GEIS* volumes included a list of published papers describing new techniques and methods. These techniques and methods were broken down into the following categories: (1) microscopy, photography and reconstruction, (2) histology and cytology, (3) operation and marking, (4) culturing (of organisms, organs, tissues and cells), (5) physiology, (6) histochemistry and cytochemistry, (7) biochemistry, (8) biophysics, and (9) mathematics. The methods listed under histochemistry and cytochemistry and biochemistry were methods that we associate with molecularization. For example, under biochemical techniques was J. E. Edström's paper, "Extraction, hydrolysis and electrophoretic analysis of RNA from microscopic tissue units (microphoresis)" (Edström, 1960). In 1961, 16 of the 57 new methods and techniques (28%) fell into one of these two molecular categories. Operation and marking and culturing had the next highest representation at 18% and 15% respectively. While the proportion of molecular methods speaks to the influence of molecularization, the relatively small number of methods papers does not directly address the bigger question of how broadly molecular methods, techniques, concepts, and approaches were being used by developmental biologists during this time period. Perhaps the editors of *GEIS* appreciated this point as well, because they introduced a second metric for designating different forms of investigation.

In 1961, the *GEIS* editors introduced a new "Key to Character of Investigation" that they applied to the projects listed in the research classification. Almost half of the projects in 1961 were assigned to one of these eleven categories of investigation. The categories were: (1) Metabolism and respiration, (2) Cyto- and histochemistry, (3) Biophysics, (4) Physical treatment, (5) Chemical treatment, (6) Influence of hormones, vitamins, growth substances, etc., (7) Biochemistry, (8) Immunobiology, (9) Electron microscopy, (10) Radio-isotope studies, (11) Cell, tissue and organ-culture. If we group cytochemistry, histochemistry, biochemistry, and chemical treatment together as molecular categories, then these molecular investigations account for 48% of the 1,530 projects classified by the "character of investigation" key. The chemical embryology of Jean Brachet, heralded as a prime example of the molecularization of development (Fantini, 2000a), is captured under these forms of molecular investigation. For instance, Brachet's project on the role of -SH groups in morphogenesis was classified as a biochemical investigation, while his project on the effects of lipoic acid on morphogenesis was classified as an investigation of chemical treatment; both projects classified as "Developmental Physiology" projects concerning the further development of Chordata (III.7.a) (*GEIS* 1961, pp. 22 & 228).

This high percentage of molecular investigations certainly speaks to the influence of molecular biology. Upon closer inspection, however, 76% of the molecular investigations occur in the

research area of "Developmental Physiology." Other research areas, such as "Descriptive and Comparative Embryology," report no molecular investigations. As a research area, "Developmental Physiology" shows almost no change in its research diversity between 1959 and 1961. Moreover, only 18% of its projects were new in 1961. The significant molecularization of this research area in developmental biology, thus, seems to be independent of the diversification or growth seen in other research areas.

Molecularization was an important element of the changes occurring in developmental biology in 1961, but was not the driver of the diversification or the growth of new projects seen across all of developmental biology between 1959 and 1961.

7. Conclusion

The records of thousands of research programs contained in the pages of the *General Embryological Information Service* provide a valuable window into the growth and transformation of research on developmental biology in the post-war period. The database that we have created from their pages has allowed us to find and characterize global patterns of growth and research diversification during a crucial period of change for the study of embryology and development. Ultimately, the information embedded in the *GEIS* periodicals has allowed us to see trends that reflect the sense of growth and innovation that may have motivated the terminology change during this period, an insight that previously rested on smaller sample sizes or what was assumed to be exemplary cases.

Our approach to understanding the wealth of data extracted from the *GEIS* volumes has been to apply tools borrowed from ecology and visualization studies to analyze the data, while appreciating the limitations of our analytic choices. By employing these methods, we are actively participating in new trends in the discipline (both in history at large and within the HPS community) that strive to apply computational and visualization tools to gain new insights about the past. We do not see our analysis, however, as trying to generate epistemologically superior explanations about phenomena like discipline formation. Instead, we see our analysis as the starting point for more detailed historical studies about developmental biology after World War II. In our view, the figures and tables we have produced help us ask more specific questions about the nature of the science at this time on a global scale.

This diversification of research, when understood in terms of the global range of patterns and processes that produced it, defies any single explanation. The diversification of this discipline was not driven solely by particular questions, such as those connected to the rise of molecular biology. Rather, a number of questions, techniques, and interests flourished during this period, including traditional areas of research like comparative and descriptive as well as new relationships with medical interests, which the growth of 'Development and Pathology' shows. It seems the term "developmental biology" did more than promote "the confluence and integration of related, but formerly isolated, lines," as Weiss claimed, but also described growth and diversification of the field as a whole (Weiss, 1959, p. ii).

The future challenge for historians with regard to these global trends is one of explaining the drivers of growth and diversification—whether they be semantic, intellectual, economic, institutional, social, or cultural. The spike in richness and diversity during a particular year, for instance, helps identify specific places, people, or ideas that we should interrogate more closely. As the example of nuclear transplantation showed, it is in these fine-grained historical investigations that we can gain more clarity about the causes that drove some of the changes in the discipline that we see reflected in the data trends. In other words, we see our analysis of the

field as a whole as complementary to, not dismissive of, micro-studies.¹⁹ Ideally, future historians of developmental biology will be able to situate their research of specific laboratories and biologists within some of these trends.

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¹⁹ Like de Chadarevian (2009), rather than pitting microstudies against big picture approaches to writing history we think that they can operate in a more complementary and informative fashion. For more discussion of the need for big picture history see also, "Focus: The Generalist Vision," *Isis* 2005.

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