Historical Essay

# Degeneracy at Multiple Levels of Complexity

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**Abstract**

Degeneracy is a poorly understood process, essential to natural selection. In the 18th and 19th centuries, the concept of degeneracy was commandeered by the colonial imagination. A rigid understanding of species, race, and culture grew to dominate the normative thinking that persisted well into the burgeoning new industrial age. A 20th-century reconfiguration of the concept by George Gamow highlighted a form of intraorganismic variation that is still underexplored. Degeneracy exists in a population of variants where structurally different components perform a similar, but not necessarily identical, function with respect to context. The presence of degeneracy increases a system's complexity and robustness against perturbations. The loss of a genetic component in biological systems, for example, can be compensated by redundant elements (the presence of isomorphic and isofunctional components), or by degenerate elements (heteromorphic variants that are isofunctional). A historical survey of the use of the term "degeneracy" reveals how and why the processes it once designated, and the mechanisms it now represents, have largely escaped the purview of contemporary science. Despite confusion and general oversight, degeneracy has been characterized by select researchers at the molecular, genetic, and neuronal levels. The concept is a potent analytical tool to understand selection, variation, and transmission.

**Keywords**

degeneracy, diversity, evolution, robustness, selection, transmission complexity, variation

September 24, 2010; revised and accepted December 8, 2010
  

Degeneration is an alteration in the structure of a pre-existing form. From the Latin word, *degeneratus*, something is said to degenerate when it "moves away from its genus or type, so that it is no longer general or typical" (Schwartzman 1994: 68). The concept of degeneracy has become a value-laden term in theology, science, and popular culture. Early developments in the colonial idea of degeneracy historically fueled the normative assumption of stable and perfect "types" within living and cultural systems. This normative assumption has remained in many spheres of human discourse as a relic of old patterns of thinking. Despite recent operational developments in the definition of degeneracy in biology, the concept has nonetheless found itself pushed to the sidelines of mainstream science because of popular misinterpretation, historical misuse, and political misappropriation of the language to talk about degenerate processes. Degeneration, once an important scientific hypothesis developed alongside the theory of evolution, has receded from view and become a lost word (Pick 1989). On account of the moral and value labels attached to the word "degeneracy," much scientific research has elided essential aspects of variation, selection, and complexity, ironically maintaining assumptions about normative identity. Consequently, fundamental processes of living systems have remained misunderstood, misrepresented, or simply unexplored. The historical potency and volatility of early degeneracy theories has most probably precluded new models from being popularized.

The early Euro-American purveyors of the concept of degeneracy "were not academic laboratory scientists; these were few in number, and as a group poorly equipped to apply and popularize an ideology of deviance" (Nye 1984: xi). Value judgments attached to the word "degeneration" proliferated during a period when deviation was misunderstood and feared. Traces of early inflections can be found in the 17th- and 18th-century Christian religious circles, which demonstrated growing concern with the "degeneracy of principles" (Sherwill 1704). Hardline religious leaders of the period considered any "departure from the standard" as corrupt, ignoble, and immoral (Willard 1673). A "degeneration" of Christianity was described as "dreadful" (Warne 1739), an "apostacy" (Wilson 1653), and a "Mark of the Beast" (Pelling 1681). A number of threats and fears fuelled anxiety about heterodoxy. In a sermon delivered in 1689 in Massachusetts Bay, Cotton Mather warned against the dangers of "degeneracy," fearing that "colonists may become barbarized, religiously dissolute" (Chaplin 2007: 52). These theological takes on the definition of degeneracy were a product of the times, and they no doubt set precedents for other misunderstandings of variation, difference, and diversity.

The negative associations of degeneration may have been catalyzed by the "almost hysterical colonial defense of custom . . . from the late 1500s onward" (Chaplin 2007: 51). Cultural reproduction and identity is often exaggerated in expatriate communities. Among the groups of displaced people, the image of homeland becomes static and fixed because it exists only in their memory and imagination. In rebuilding a culture abroad, memory serves as a guide, and any departure from previous cultural integrity can be feared. Among the colonies of the British Empire, for example, the mother country remained their most important cultural reference. In the reproduction of culture, laws, and customs, deviation was shunned. Not surprisingly, negative connotations of degeneration developed alongside the growth of colonial empires.

The early modern English tended to regard changes in custom, religion, and language as evidence of degeneration. Continuity was greatly preferred, whether in pedigree, text, ceremony, or law. Degeneration could take two forms: a fall from an original and pure type, or the accretion of elements from religious or cultural inferiors through the acquisition of pagan rites or barbarian customs. (Chaplin 2007: 51)

In 1574, the Spanish royal cosmographer, Juan López de Velasco, used the word "degenerated" in a very strategic way when he came up with a climatic theory to explain the adaptation of the Spanish to different natural and social environments in the New World (Boyd-Bowman 1971: 19–20). Velasco wrote that extended stays in these foreign climates would change physical and spiritual attributes: ". . . manners and social intercourse have degenerated, and affect more quickly those with less powers of virtue; and therefore there has always been and still is much calumny and uneasiness among the people" (quoted by Palmié 2007: 68). López de Velasco had used the idea of degeneration to denote degradation. If the colonizing culture was seen as the height of civilization, then any alteration necessarily constituted decay. In some ways, his view of degeneration anticipated a dramatic political and scientific discourse that would ensue in centuries to follow.

However, not all seafarers used the word "degeneration" to criticize non-Europeans. In the *Mercure de France* published in 1769, Philibert Commerçon, a French naturalist who sailed with Louis-Antoine de Bougainville on board the Boudeuse, offered a description of the society of Tahiti as the state of natural man before it had degenerated into reason. Although Commerçon saw degeneration as flowing from natural to civilized, the fear of the civilized man degenerating into savagery was to become more prevalent.

In 1748, the groundwork for a theory of degeneration was laid out in a book, *Relación histórica del viaje hecho de orden de su Majestad a la América Meridional* (Historical Treatise of the Trip to Southern America Done by Order of his Majesty), by a Spanish naval officer, Don Antonio d'Ulloa. D'Ulloa's thesis, which influenced the ideas of later thinkers such as Lamarck and Buffon, contended that "the human condition in the Americas was degenerate[d] as a result of a long history of colonialism, slavery, exploitation of natural resources and subjugation of the native peoples" (Thomson 2008: 200).


**Figure 1.**
A statue of Georges-Louis Leclerc, Comte de Buffon, in the Jardin des Plantes in Paris, France. Photo by Paul Mason, 2010.

Degeneration, as a theory of nature, was first brought to the sciences by Georges-Louis Leclerc, Comte de Buffon, a well-known and influential writer of the natural sciences in the Age of Enlightenment (see Figure 1). Buffon believed that in nature only individuals exist and, unlike Linnaeus, he did not consider the species as a collection. For Buffon, species were those organisms whose sexual propagation produced only their kind. In contrast to the classificatory system of Linnaeus that grouped animals by "broad and variable characteristics" (Koerner 1996), Buffon understood nature as an "unbroken continuum of individuals" (Sloan 1976). According to Buffon (1749: 10a–b) the classes that Linnaeus imposed were imaginary because "it is impossible to give a general classification, a perfect systematic arrangement, not only for Natural History as a whole, but even for a single one of its branches."

Buffon explained some of the variability he saw in nature as a product of degeneracy. As a creationist, Buffon believed that all animals descended from early prototypes originating from a center of creation to which they were ideally suited. Degeneration over successive generations allowed for the emergence of different races of animals, all from a single rootstock, whose preferred habits over time variously affected their distribution. He also argued that species must have degenerated after climate change and the activities of mankind spread those species away from an origin of creation. The term "degeneration" was employed to describe the bodily changes manifested in migrating populations who had abandoned their ideal environment for new and more difficult habitats.

In the fifth volume of his 44 volumes of natural history, Buffon drew comparisons between wild animals in Europe and the New World, as well as domesticated animals exported to the New World. He reported that such animals had degenerated and were smaller. Buffon believed that race was pliant, inflected by the conditions of the environment. For example, he regarded Native Americans as a degenerative variety of humans. Buffon made claims based on incomplete and imperfect data from abroad, and Eurocentrism dominated his ideas about degeneracy. His perspective was a response to the growing technological, military, and economic might of Europe, which, together with the devastating impact of Eurasian disease in the New World, only contributed to an impression of racial supremacy. While Buffon's concept of species is much closer to the modern than Linnaeus', Buffon's theory of degeneration met with intense controversy. As a scientific hypothesis, degeneration attracted vehement opposition from people living in the New World, most notably from Jefferson (1982), who, among his many rebuttals, published a challenge to Buffon's ideas in 1787.

In volume 14, Buffon observed that despite similar environments, different regions have distinct plants and animals. Variations, in Buffon's opinion, were more likely a consequence of degeneration than specific adaptations (David and Carton 2007). His ideas brought special attention to the definition of species and the issue of intra-specific variability, something his scientific successors were left to tackle. Despite certain limitations, Buffon did provide some remarkable insights for his time. His concept of the degeneration of species had a considerable influence on the thinking of later writers on natural history such as Darwin and Lamarck and was echoed in the works of Anton Dohrn and Edwin Ray Lankester.

The idea that some attributes constitute a "normal type" is a 19th-century concept that "became conflated with historical notions of the ideal body" (Vertinsky 2002: 96). Scientists, doctors, and writers associated normality with the absence of pathological symptoms in the organs, variation could only be detrimental, and abnormality became entangled with the concept of degeneracy (Rajchman 1988: 101). By the second half of the 19th century, "degeneration" became a pervasive term throughout European culture that grew to be as widespread and encompassing a term as evolution (Chamberlin and Gilman 1985). Around the same time that Darwin published *The Origin of Species*, the French psychiatrist Morel (1857) put forward his definition of degeneracy as, "a morbid deviation from an original type" (p. 5). While Buffon had believed that the simple physiological alterations of degeneration did not transform human nature, Morel argued that biological alteration entailed ontological mutation (Pick 1989: 60). Morel's (1857) theory of degeneracy constituted the first total etiologic theory of madness that made it possible to insert psychiatry within the framework of medicine (Schweitzer and Puig-Verges 2005). His theory functioned almost like dogma until World War I (Postel 1998). In 1974, Foucault (2006: 222) labeled Morel's concept of degeneration as "great" but "unfortunate." He distinguished degeneration from the Theory of Evolution in both conception and 20th-century interpretations. Foucault (2006) notes that it was Magnan (1893) who coupled Morel's theory with the notion of evolution and introduced a reference to the neurological localization of the degenerative process.

Inspired by Morel's work, a German journalist, philosopher, and practicing physician, Nordau ([1892] 1968), rendered the concept of degeneracy fashionable in his widely translated book, *Entartung*, published in English as *Degeneration* (1895). According to Nordau ([1892] 1968: 22), degeneracy was a mental and social disease where the individual is "incapable of adapting himself to existing circumstances. This incapacity, indeed, is an indication of morbid variation in every species, and probably a primary cause of their sudden extinction." Nordau's interpretation of degeneracy was profoundly tainted with conventional ideas of order and disciplined progression typical of the late 19th-century European middle class. *Entartung* captured significant public attention and was celebrated in some circles (Pick 1989: 25). The book was a sensation in Germany, quickly translated into French, ran into seven editions in six months in America and England (Greenslade 1994: 120), and went through as many editions in Italian as it did in the original German (Mosse 1968: xiv). The book was only a short-lived sensation though (Mosse 1968: xv). Nonetheless, Nordau's interpretation of degeneracy persisted in Western society (Mosse 1968: xxxiii).

Contemporaneous to Nordau's *Entartung* were the less celebrated works of Anton Dohrn, founder and first director of the Stazione Zoologica, Naples; and Edwin Ray Lankester, Fellow of Exeter College, Oxford. In 1875, Dohrn proposed "the hypothesis of Degeneration as capable of wide application to the explanation of existing forms of life" (Lankester 1880: 29). According to Dohrn's hypothesis, forms diverge and become functionally degenerative, life evolved through a kind of metamorphosis of nature, and certain forms were thought of as degenerating groups (Breidbach and Ghiselin 2007: 175). In his book, Lankester (1880) stated that Dohrn's hypothesis deserved recognition and merit and so presented his own detailed analysis showing the loss of certain anatomical structures and their modifications in animals. Modified organisms, according to Lankester (1880: 39), were "degenerate descendants of very much higher and more elaborate ancestors." Lankester (1880) understood natural selection to act on the structure of an organism, to keep it in status quo, or to increase or diminish the complexity of its structure. His descriptions alluded to a hierarchical understanding of the animal kingdom as opposed to the intricately interconnected ecology that we now understand it to be. At the time of their work, Dohrn's and Lankester's positions were unsurprisingly anthropocentric and still displayed influences of religious thought. Dohrn's propositions suggested that all animals were really degenerate descendants of an originally perfect humanity, and Lankester (1880) suggested that degeneracy should be defined as a return from complexity to simplicity (Pick 1989: 173). Their perspectives unified an understanding of evolutionary change with an assumption of initial perfection. Change or variation was necessarily a degradation. This pre-modern constellation of concepts led to our enduring popular understanding of degeneration.

Dohrn's and Lankester's explanations were steeped in the world views of their time. The subsequent work of American medical and dental practitioner Eugene S. Talbot consolidated this interpretation. In Talbot's 1898 book, *Degeneracy: Its Causes, Signs and Results*, he associated degeneration with contagious and infectious diseases, destructive behavior, toxic agents, unfavorable climate, mental decline, consanguineous and neurotic intermarriages, juvenile obesity, impure food, arrested development, skeletal anomalies, sensory deterioration, paranoia, hysteria, idiocy, and one-sided genius, as well as social parasitism, moral degradation, and cultural demise (Patrick 1899). All social ills were degenerations from a presumed ideal. By the end of the 19th century, despite the best efforts and expressed desire to resolve the conceptual questions, degeneracy was not successfully reduced to a fixed axiom or theory (Pick 1989: 7).

While Buffon (1753) had suggested that we may be driven to admit that apes are a degenerate man with whom we share a common ancestor, in 1901 the American logician Peirce predicted (1979: 17–18) that one day a writer would describe man as a "degenerate monkey." A quarter of a century after Peirce's prediction, that writer appeared. Lodewijk Bolk, an anatomist and founder of modern physical anthropology in the Netherlands, read a paper before the 1926 meeting of the Anatomical Society in Freiburg entitled "The Problem of Human Development" (see Weyl 1959; Baljet 1997). In his paper, Bolk detailed his retardation theory, claiming that humans are a "degenerate monkey" incapable of normal development and an obstacle to nature (Chwistek and Brodie [1948] 2000: 5). The proposition was met with considerable opposition by Bolk's contemporaries, but today evolutionary theorists of human neoteny support a sympathetic position (e.g., Gould 1977; Shaner and Hutchinson 1990; Verhulst 1999; Deacon 2010). Recently, sociologist Halton (2008) revived Peirce's phrase, "degenerate monkey," to emphasize that we are prematurely born with few developed instinctive capacities that require socializing attunements over a prolonged period of development before we reach maturity.

By the middle of the 20th century, Richard Walter from the Division of Neurology, University of California, Los Angeles, noted the neglect of degenerate processes (Greenslade 1994: 11). "The Phenomena that degeneracy attempted to explain are still of great current interest and far from completely understood . . . . Any concept that has been used for explanations in so many connections probably deserves interest . . . " (Walter 1956: 429). More than 50 years later, especially in the light of genetic evidence, Walter's suggestion has become even more imperative.

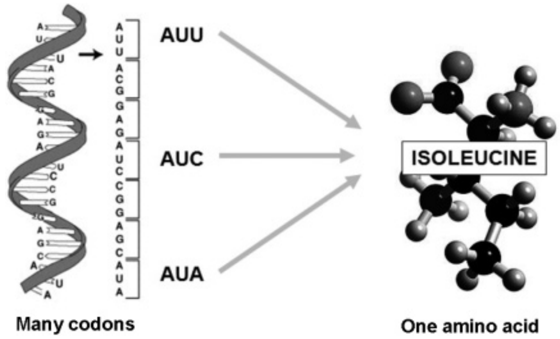


**Figure 2.**
In genetics the term "degeneracy" describes a scheme where several different base sequences (i.e., two or more different nucleotide triplets) can code for one amino acid. In this example, Adenine (A), Uracil (U), and Cytosine (C) in different combinations can code for the amino acid Isoleucine.

**Table 1.** Degeneracy is observed in a system if there are components that are structurally different (nonisomorphic) and functionally similar (isofunctional) with respect to context. In contrast, redundant elements are isomorphic and isofunctional regardless of the context. Degenerate components can also be pluripotential because they can change their function according to context.

| | | Context independent | |
|---|---|---|---|
| | | **redundant** | **(unspecified)** |
| Context dependent | **degenerate** | isofunctional | nonisomorphic |
| | **pluripotential** | isomorphic | nonisofunctional |

Walter was likely unaware of a novel contribution to genetics being made by his contemporary George Gamow, a Ukrainian-born American scientist, mathematician, and theoretical physicist who introduced a "new idea" in 1954 to molecular biology and genetics (Crick 1955). Gamow played a key role in decoding the genetic script. This script is composed of chromosome fibers made up of deoxyribonucleic acid (DNA), and has a central role in building proteins out of amino acids. After learning that DNA consists of only four different kinds of nucleotides (Watson and Crick 1953), Gamow suggested that some amino acids were recognizable by two or more different nucleotide triplets (Figure 2). The coding of amino acids by more than one nucleotide triplet is called degeneracy. Gamow's description of degeneracy offered an explanation as to how the 64 triplet codons of the four bases in DNA were able to specify 20 odd amino acids (Woese 2001). Gamow's original idea became an essential feature of the final solution to the coding problem of DNA (Harper 2001). What Gamow and his contemporaries may not have realized is that degeneracy at other levels of complexity may be just as important in phenotypic evolution as degeneracy at the nucleotide level (Lynch et al. 2001). By describing degeneracy as the way different configurations of biological structures can produce the same outcome, Gamow had stumbled upon a crucial component for understanding the processes of natural selection. When there are structurally different features that have the same function, selection can sort these structures differentially.

Austrian physicist Schrödinger (1944) paved the way for Gamow to think of chromosome fibers as being a code-script (Doyle 1997: 41), and Gamow, in turn, laid the foundation for the genetic code to be understood as a degenerate. The concept of degeneracy in physics is a value-free term, but when the term was imported into biology it became reunited with a great deal of historical baggage. This historical legacy has unfortunately prevented theorists from engaging with an important concept in evolutionary theory. Due to negative value judgments frequently attached to the term "degeneracy," we don't properly appreciate the forms of variation the term labels.

## A Value-Free Scientific Definition of Degeneracy

The biologically useful definition of degeneracy refers to how systems are coded or mapped (Levine 2004). Degenerate components have a structure-to-function ratio of many-to-one (e.g., Figure 2). Degeneracy is often confused with redundancy, which occurs when the same function is performed by structurally identical elements. Redundant elements are duplicate copies that have a structure-to-function ratio of one-to-one. Unlike redundant elements, degenerate elements can be pluripotential, and produce different outputs under diverse conditions. Degenerate elements may share the same function, but unlike redundant elements, they do not share the same overall structure, so they increase complexity and robustness in a system. The function of degenerate components is not easily deleted from a system because the function is distributed among a population of dissimilar structures (see Table 1).

Trait selection requires more than one structure from which to select. The presence of two or more different ways of doing the same thing or encoding the same information is crucial for an evolutionary system. This degeneracy means that an organism can vary without compromising function. It creates the potential for variation and ensures the organism against perturbations. In addition, it installs greater pluripotentiality underlying functional continuity for future deployment. As the system evolves, it can become less fragile in the face of its own variation. Degeneracy creates a surplus of structures for later exaptations.

Without degeneracy, there can only be selection by competitive elimination. If a function is subserved by identical structures, then this function is either preserved or eliminated by selective pressures. Constantly removing variation from a population through changes in context and selective pressures would inevitably lead to the extinction of redundant variants. The accrual of intraspecific variation through the presence of different isofunctional structures provides robustness and allows a system to be maintained far-from-equilibrium. Thus, degeneracy is necessary for the operations of variation and selection in complex organisms (Tononi et al. 1999; Edelman and Gally 2001). Degeneracy is one of the inescapable mechanisms of natural selection that is essential for the evolutionary process.

Selectional systems would be likely to fail without degeneracy (Edelman 2006a: 33). Formerly, researchers had difficulty explaining how backup properties could be exposed to selection pressures and favored to spread in populations (Frank 2003). Only recently have researchers been able to understand how degeneracy has been selected (Thomas 1993; Brookfield 1997; Nowak et al. 1997; Dall and Cuthill 1999; Woollard 2005). Living systems have no a priori design on how to survive, and selection has no way of assigning responsibility to particular gene loci. Degenerate systems are maintained and favored because, in general, different gene networks contribute to each phenotypic feature (Tononi et al. 1999; Green et al. 2006). In different contexts, a degenerate system has the potential to produce different outputs and thus exhibits adaptability in the face of changing and novel environmental demands.

The revised 21st-century scientific definition of degeneracy is operational and neutral. The concept has been used most prominently in Edelman's theory of neuronal group selection (Edelman 1987). The brain is a "selectional system in which huge repertoires of variant circuits arise dynamically within the connections provided by neuroanatomy" (Edelman 2006b). The developing brain possesses an initial oversupply of neurons. The combinatorial possibilities, which exist within and between neuronal groups, are a source of variation that allows the processes of selection to operate. Those neuronal groups that can perform the same function without sharing the same underlying structure are degenerative. The example of a neurological lesion that appears to have little effect within a familiar context reveals the presence of a degenerate backup system (Tononi et al. 1999). Degeneracy contributes to the overall complexity and robustness of a system and requires a certain level of functional redundancy to be operational. The existence of degeneracy has been identified at various levels of complexity; from the cellular and molecular (Edelman and Gally 2001; Cohen et al. 2004), to the genetic (Goodman and Rich 1962; Reichmann et al. 1962; Weisblum et al. 1962; Barnett and Jacobson 1964; Weisblum et al. 1965; Mitchell 1968; Konopka 1985; McClellan 2000; Gu et al. 2003), neural (Edelman and Gally 2001; Noppeney et al. 2004; Leonardo 2005), and cognitive levels (Price and Friston 2002; Friston and Price 2003; Edelman 2004; Noppeney et al. 2004).

Taylor's (2001) extensive analysis of distributed agency within intersecting ecological, social, and scientific processes is a notable example of degenerate dynamics. He discusses how the contingent outcomes of intersecting processes operating at different spatial and temporal scales contribute to the heterogeneous construction of a situation. Taylor (p. 314) sees depression, for example, not as a condition, but as a temporary configuration of multiple contributing elements that takes place along the multistranded life course of an individual. He demonstrates that for any given situation there are alternative routes to reach the same end. For example, he describes pervasive erosion in a mountainous agricultural region in Mexico as the result of human illness, population change, and changing land practices in the 16th century, and changing economic arrangements, work relations, and social organization in the 20th century. The net flux of a variety of interacting elements in multifarious arrangements can give rise to the same situation. Outcomes are not endpoints but snapshots of ongoing engagements between intersecting processes. Elements imbricated in one construction process are implicated in many others.

Taylor's (2001) discussion of heterogeneous construction is a way of conceptualizing degenerate processes. His approach puts aside top-down and bottom-up accounts in favor of models that include both bottom-up and top-down processes with intermediate complexity. Agency in a heterogeneously constructed system is distributed with the sources of causal influence varying at each level. The significance of each factor on any particular outcome is contingent upon the state of the rest of the system; for example, whether a traumatic life event causes depression depends upon the resilience of the individual and other contributing social factors. Just like contemporary theorists of degeneracy, Taylor identifies that the contingent intersection of different processes in a structural network ensures ongoing change and restructuring. Organisms give rise to descendants that differ from them because structure is subject to contingent events leading to internal differentiation. Taylor's framework is an operational conceptualization of the ongoing dynamics of a degenerate system.

In biological sciences, the amplification and preservation of structural duplication is understood to increase long-term opportunities for the evolution of new gene functions (Force et al. 1999). Redundancy creates the opportunity for degeneracy to arise. The function of the original structure is maintained by one copy, while any other copy is free to diverge functionally. A second avenue for degeneracy to emerge is through parcellation, where an initial structure is subdivided into smaller units that can still perform the initial function and can also be functionally redeployed (Budd 2006: 617). A third avenue of degeneracy is through synergistic structures that perform a function in combination (Budd 1998). If one structure is able to perform the initial function independently, the other one is open to modification. A fourth form of degeneracy can occur when two independent structures converge upon the same function, eventually allowing a shift in either structure, provided the necessary function is maintained (e.g., Budd 1999).

In summary, once essential functions are in place, the least constrained structures can change.

Budd's work highlights that studying degeneracy is vital to understanding the ways in which compound characters are allowed to change (Budd 2006: 614). Contemplating morphological transformations during the Cambrian, Budd (1998) demonstrates that evolutionary shifts do not involve saltational functional discontinuities, but that functional transitions involve preadaptation, functional degeneracy, and changes in interactions between various functional parts. Mathematical modeling has shown that the interplay of degeneracy and selection can lead to a "clumped" distribution of traits and a disappearance of intermediate forms giving the appearance of quasi-saltational transitions (Atamas 1996; Atamas 2003; Atamas and Bell 2009). Thus, instead of stating, "the cellular machinery that evolved before and during the Cambrian was highly generative" (Hauser 2009: 190), we are probably better off enquiring how the cellular machinery during this period was highly degenerative.

Deacon (2010) identifies degeneracy as an intraorganismic, evolution-like process integral to the evolution of human language. He describes humans as a self-domesticated species with loosened survival demands and a susceptibility to social control and experiential modification. While Darwin (1871) believed domestication had deleterious consequences because selective pressures were relaxed, Deacon (2010) demonstrates that the evolution of language is actually a positive consequence of fewer constraints, functional redistribution, and the long-term adaptation of an array of flexible developmental mechanisms at the neurological, behavioral, and social levels. In addition to explaining internal redundancy (structural duplication), Deacon explains external redundancy (functional duplication) and global external redundancy (functional redistribution or dedifferentiation), both of which can be thought of as different types of degeneracy.

An example of external functional duplication is the loss of endogenous vitamin C synthesis in some lineages (Deacon 2010: 9004). Function does not necessarily have to be performed solely by internal structures. Function can be simultaneously performed by endogenous and exogenous structures. Exogenous resources can complement endogenous production. Conversely, endogenous structures can be called upon to compensate for a decline in exogenous resources. Thus, degenerate processes can be distributed between internal and external structures. Degeneracy, in this sense, may be a useful concept for scholars of the extended mind (see Clark and Chalmers 1998). If genetic control is offloaded onto epigenetic processes, then innate abilities, such as birdsong (Deacon 2010: 9004–9005), can be globally redistributed onto an array of ontological systems that each fractionally influences the outcome.

Deacon (2010) describes the intraorganismic processes of selection as characterized by replication, variation, and differential preservation (selective retention or elimination). These processes have counterparts in redundancy (multiple copies of the exact same replicator), degeneracy (multiple copies of structurally different replicators), and functional interdependency (the distribution of function across multiple synergistic replicators). As a system becomes more complex, it simultaneously becomes more functionally redistributed by structural variation. Degeneracy allows for a relaxation of selective processes that subsequently provides the space for replicators to incrementally deviate from their antecedent function. The relaxation of selection reduces competitive elimination and favors the preservation of structural variants. Within certain degrees of freedom, there can be a random exploration of adjacent function space. However, if a deviant replicator enters into a related interaction relationship with a duplicate counterpart, then selective processes can be reintroduced and act upon deleterious or synergistic interactions. According to Deacon's reasoning, the involvement of neural circuitry and the increased importance of social transmission in the determination of human language is a product of functional degeneracy. Global redistribution effectively offloads a significant degree of genetic determination onto epigenetic processes. The neuroepigenetic variants of selection are one of many intraorganismic morphodynamic processes that open a system to experiential modification and provide a greater degree of freedom for the influence of social transmission. Deacon is led to hypothesize that the social history of language exhibits evolvability and robustness because of redundancy, degeneracy, comparative redistribution, and the recruitment of multiple levels of intraevolutionary mechanisms (e.g., genetic, neuronal, and social processes). His description of degeneracy at intersecting levels of complexity stands free of historical value biases, and demonstrates that human uniqueness does not necessarily arise by positive natural selection because certain cognitive skills are beneficial to ancestral hominins.

## Reflections on the Past

The history of the use of the term "degeneracy" is not linear, but followed many trajectories that have collectively associated it with degradation, implied a disdain for heterogeneity, and reinforced uniform-type notions. Correspondingly, degeneracy as intraorganismic variation became an increasingly overlooked part of scientific investigation and theory. Natural selection as a prime cause of evolution did not become widely accepted until about 1940, after it had been successfully integrated with genetics (Quammen 2009). By this time, mainstream scientific circles avoided the concept of degeneracy because it fell into disrepute, especially with the discrediting of eugenics. A history of the popularization of the term "degeneracy" is more than just a biography of a word. A historical account highlights how underlying mechanisms of living systems have gone unexplored because normative thinking blinded our intellectual predecessors to variation, and because a key concept to discuss variation suffered guilt by association.

Anthropologists have often assumed culture to be a uniform entity without considering the array of variable characteristics within cultural systems. Sociologists have also found themselves guilty of viewing culture as "unitary and internally coherent across groups and situations" (Dimaggio 1997: 264). Static notions of the "cultural type" lead to uniform models of cultural transmission without variation. Wallace (1970), in contrast, advocated emphasizing diversity and found it more interesting to consider the actual diversity of habits, motives, personalities, and customs that coexist within the boundaries of any culturally organized society. However, he noted the following:

> In many investigations, the anthropologist tacitly, and sometimes even explicitly, is primarily interested in the extent to which members of a social group, by virtue of their common group identification, behave in the same way under the same circumstances. For the sake of convenience in discourse, they may even be considered to have learned the "same things" in the "same cultural environment." Under such circumstances, the society may be regarded as culturally homogeneous and the individuals will be expected to share a uniform nuclear character. If a near-perfect correspondence between culture and individual nuclear character is assumed, the structural relation between the two becomes nonproblematical, and the interest of processual research lies rather in the mechanisms of socialization by which each generation becomes, culturally and characterologically, a replica of its predecessors. (Wallace 1970: 22)

Since the 1980s, anthropologists have been critical of culture concepts. They have critiqued culture (Marcus and Fischer 1986), written "against" culture (Abu-Lughod 1991), and "beyond" culture (Gupta and Ferguson 1992). They have also foretold the "breakdown" of culture (Fox 1995) and the "demise" of the culture concept (Yengoyan 1986). Clifford (1988) and Goody (1994) have even proposed abandoning the notion of culture altogether, in part because observable variation, change, and internal conflict is inconsistent with a model of unchanging norms. Anthropologists have recently found the necessity to counter understandings of culture that designate a distinctive way of life of a discrete and clearly bounded social group. This usage of the culture concept has been criticized as retaining "some of the tendencies to freeze difference possessed by concepts like race" (Abu-Lughod 1991: 144) and for being deployed in a colonialist or discriminatory way by "Western" subjects onto "non-Western" others "in ways so rigid that they might as well be considered innate" (Abu-Lughod 1991: 144). Brightman (1995) and Brumann (1999), among others, have demonstrated that this view of culture has not been as endemic to anthropology as some, like Abu-Lughod (1991), have suggested, but when deployed at any strata of society, the culture concept can have extensive repercussions. A tendency to essentialize the constructs of culture "has been appropriated by people other than anthropologists in the wider community and it has been deployed in ways reminiscent of the race concept" (Dominguez 2007: 216). While anthropologists have not abandoned the notion of culture, they "find themselves in the process of reappraising, correcting and enriching their comprehension of culture and society thanks to the lessons learned . . . " (Dominguez 2007: 215). As Buffon (1749) contradicted Linnaeus' definition of species because it was artificial, arbitrary, and made broad classifications of type based on individual traits, so too must we reframe our understanding of culture with a more fluid, mutable, and holistic model based on degenerate representations.

Our internal representation of culture is formed from a collection of disparate bits of information that we experience nonetheless as a unitary phenomenon. Sperber (1996: 118) suggests that despite the large amount of variation in cultural representations, we still persistently discern stable cultural types for the following two reasons:

> First, because, through interpretive mechanisms the mastery of which is part of our social competence, we tend to exaggerate the similarity of cultural tokens and the distinctiveness of types; and second, because, in forming mental representations and public productions, to some extent all humans, and to a greater extent all members of the same population at any one time, are attracted in the same directions.

Anthropologists such as Wallace (1956) have long suspected that we experience culture as a gestalt. Wallace noted that periods of extreme stress upon individual members of a society could lead to further routinization and stabilization of cultural activity. Drawing upon growing ethnographic data from five continents, and with a particular attention to a 19th-century Native American religious movement, Wallace observed that "deliberate, organized, conscious effort by members of a society to construct a more satisfying culture" is dependent upon persons who "perceive their culture . . . as a system" (p. 265). The persons involved take action to preserve the constancy and integrity of the matrix of their perceived system, ". . . by maintaining a minimally fluctuating, life-supporting matrix for its individual members" (p. 265). When such actions, behaviors, and ways of thinking become historically propagated, it reinforces and strengthens notions of culture as a closed system.

Wallace's ideas map onto the colonial experience almost seamlessly, but colonialists were not the only people to have rigid ideas of species, race, and cultural type. "Cross-cultural evidence," that Atran (1990) points out, "indicates that people everywhere spontaneously organize living kinds into rigidly ranked taxonomic types despite wide morphological variation among those exemplars presumed to have the nature of their type" (p. 71). More wide-ranging research about the psychological origins of the normative assumption of cultural types can be found in the work of Richter and Kruglanski (2004). These researchers have highlighted how the psychological need for closure is a key factor in the formation of stable cultural representations (Richter and Kruglanski 2004: 104). The need for closure is a response to stressful conditions and uncertainty. It is a motivational impulse that can elicit premature and unmoving adherence to the most highly visible constructs centered around pervasively accessible cultural norms and ideals. In a discussion about the relationship between the need for closure and cultural patterns, Richter and Kruglanski (2004) describe that when a group judges outgroup members predominantly on the basis of stereotypes, it creates a perceived homogenization of the out-group and simultaneously a homogenization of the in-group (Richter and Kruglanski 2004: 108). In such a scenario, diversity in cultural traits is reduced. In-group favoritism and out-group derogation asserts common values among members, builds shared realities, and reinforces consensus. At the extreme, a group whose members are under a heightened need for closure are more likely to centralize their decision-making structures (Richter and Kruglanski 2004: 112). They evidence the tendency toward authoritarianism in German society in the earlier part of the 20th century and the rise to power of Hitler as a case where an autocratic leadership structure emerged among members of a cultural group who were in high need of closure (Richter and Kruglanski 2004: 113). Swept up by such forces, degeneration is a concept that became heavily value-laden, simplified, and a clear marker of the normative thinking of society.

In its most disastrous application and gross misuse, the degeneracy concept was politicized by the Nazis, who in their delusions of eugenics, desire to eliminate "inferior races," and efforts to "sanitize culture," used the concept of degeneracy to justify their genocide. For the Nazis, degeneracy was contemptuously equated with waste, nonconformity, and vagrant social classes. Their inability to accept and recognize the importance of variation was the very antithesis of what we now understand degeneracy to be. The sentiments of Hitler and the Third Reich, according to Greenslade (1994: 263), could have come straight out of Nordau's *Degeneration* ([1892] 1968). The Minister of Justice under the Third Reich, Hans Frank, defined degeneracy as

> an immensely important source of criminal activity . . . in an individual, degeneracy signifies exclusion from the normal "genus" of the decent nation. This state of being . . . , this different or alien quality, tends to be rooted in miscegenation between a decent representative of his race and an individual of inferior racial stock. (Frank 1938, cited by Pick 1989: 28)

Degeneracy as a scientific hypothesis arose during a period when cultural diversity was shunned and conventionality was promoted. At the pen of popularists like Nordau, degeneracy moved from being a scientific hypothesis to a cultural metaphor that reflected the values, anxieties, and world-views of imperialist societies. Nordau's theory of degeneration flourished during a period when the capitalist system was still growing and progress was the order of the day. Any deviation from the standard—a degeneration—was seen as an impediment to productivity and achievement.

Since World War II, the word "degeneracy" has largely disappeared from evolutionary discourse because of the association with discredited ideas. Ironically, regardless of the best-intended attempts to correct and erase the dangerously conformist behavior that arose from a flawed misappropriation of degeneracy, our productivist and consumerist lifestyle has still nonetheless managed to replace diversity with standardization. The negative controls of Nazi murder and mutilation have been substituted by the positive controls of materialism and consumerism as the drivers of homogeny. Though categorizations of normalcy and degeneracy may be dismissed in theory and are often pilloried for their reactionary, racist, and eugenicist subtexts, the notion of the standard type maintains a strong, subliminal, and enduring influence in prescriptive modes of education, medicine, and popular culture. Old words may be shunned, but normative practices persist nonetheless. As the growth of industry, consumerism, and urbanization increasingly challenges biodiversity, we may need to reevaluate how we nurture degeneracy in modern societies.

Biological degeneracy, in the Gamowian sense, is observable at multiple levels of complexity: from genetic codes to neural systems. In a recent paper on antigen-receptor degeneracy, where single antigens are understood to bind and respond to many different ligands, the authors reflect that degeneracy seems like a strangely derogatory term for such virtuosic multi-functionality (Cohen et al. 2004). These authors open their paper by referring to a definition of degeneracy provided in the Oxford English Dictionary (Second edition, 1989)—which associates degeneracy with decline, debasement, and degradation—and ask: "Is the slur apt? Is nature herself debased, or is it only that our expectations of her have been disappointed?" Their perceptive questions are partly answered by history but also partly allude to deeper philosophical dilemmas. At the scientific level, these authors understand that degeneracy is not an ignominious dilapidation from a higher to a lower form. Yet, despite determining that degeneracy at the molecular and cellular levels is an indispensible part of complexity and evolution, these authors conclude their paper by stating, "Degeneracy is blameworthy when it comes to human behavior." Evidently, the idea of behavioral and cultural degeneracy still reignites old preconceptions. The terminology we use to describe the natural world can prove to be fateful. The term "degeneracy" is an evidence of how scientific terminology can bleed inappropriately into common usage, and how popularization of certain ways of using a word can rebound back upon scientific understandings.

The revised 21st-century scientific definition of degeneracy based upon Gamow's description is free of the preconception that degeneracy is necessarily "dreadful," "morbid," or "an apostasy." Researchers have recognized the necessity to develop a better understanding of degeneracy at the molecular and cellular levels (Cohen et al. 2004), as well as at the neuronal level (Price and Crinion 2005). Perhaps we can also extend this obligation to the behavioral and cultural levels. The most recent modeling of complex adaptive systems (Whitacre 2010; Whitacre and Bender 2010) suggests that the role of degeneracy in distributed robustness, evolvability, and multiscaled complexity could be much greater than earlier predictions (Edelman and Gally 2001). Once we eliminate the 18th- and 19th-century contamination and biases that have plagued our understanding of deviations, divergence, and change, we can remove the baggage of parochialism that has confined science, limited the scope of investigations, and restricted the import of research in this area.

## Acknowledgments

The author thanks Ryszard Maleszka for his ongoing support, counsel, and advice, Juan Dominguez for analytical discussions, Greg Downey for his thorough and in-depth critical feedback, as well as Daniel Drumm, Casimir Macgregor, Robert Rudegeair, John Sutton, Hans and Hedwig, and the editorial staff of *Biological Theory*, Werner Callebaut and Deborah Klosky. This research was supported by an Australian–Netherlands Research Collaboration Travel Fellowship, a Macquarie Research Excellence Scholarship, and the Macquarie Postgraduate Research Fund (Deputy Vice Chancellor's Commendation), Macquarie University.

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