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Between holism and reductionism: a philosophical primer on emergence

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Ever since Darwin a great deal of the conceptual history of biology may be read as a struggle between two philosophical positions: reductionism and holism. On the one hand, we have the reductionist claim that evolution has to be understood in terms of changes at the fundamental causal level of the gene. As Richard Dawkins famously put it, organisms are just 'lumbering robots' in the service of their genetic masters. On the other hand, there is a long holistic tradition that focuses on the complexity of developmental systems, on the non-linearity of gene–environment interactions, and on multi-level selective processes to argue that the full story of biology is a bit more complicated than that. Reductionism can marshal on its behalf the spectacular successes of genetics and molecular biology throughout the 20th and 21st centuries. Holism has built on the development of entirely new disciplines and conceptual frameworks over the past few decades, including evo-devo and phenotypic plasticity. Yet, a number of biologists are still actively looking for a way out of the reductionism–holism counterposition, often mentioning the word 'emergence' as a way to deal with the conundrum. This paper briefly examines the philosophical history of the concept of emergence, distinguishes between epistemic and ontological accounts of it, and comments on conceptions of emergence that can actually be useful for practising evolutionary biologists. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, ••, ••–••.

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'Emergence' is a controversial concept with a convoluted history, in both science and philosophy. It is therefore not surprising that it has been misused and vilified, as well as more often than not misunderstood. Typically, the idea of emergence is brought up by researchers who are – for one reason or another – unhappy with an ultra-reductionist scientific programme, preferring instead some kind of holism or interactionism in the way they approach their research questions (think of the always current debates on gene–environment interactions: Lewontin, 1974a). Just as surely, biologists who are embedded in reductionist programmes are skeptical of emergence and similar ideas as obscurantist and leading only to never ending and fruitless debates – think, say, of Richard Dawkins' (1976) dismissal of anything smelling like group selection, or his famous quip that living organisms are nothing but 'lumbering robots' controlled by their selfish genes.

It is undoubtedly the case that methodological reductionism has an enviable track record both in biology specifically and in science more generally. By the onset of the 20th century chemistry had already for all effective purposes been reduced to physics (Le Poidevin, 2005; although this is by no means an accepted conclusion in philosophy of chemistry: Hendry & Needham, 2007), and hopes were high that biology would soon follow suit. Indeed, the demise of vitalism and the contemporary surge of

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model-based genetics at the beginning of the 20th century seemed to nail the argument in favour of reductionists. In 1931 J. B. S. Haldane could confidently declare that ‘Biologists have almost unanimously abandoned vitalism as an acknowledged belief’, although he was at the same time unconvinced by exclusively mechanistic explanations of biological phenomena: ‘We must find a different theoretical basis of biology, based on the observation that all the phenomena concerned tend towards being so coordinated that they express what is normal for an adult organism’ (cited in Bedau & Cleland, 2010: 95).

The Modern Synthesis (MS) of the 1930s and 1940s was, in some important respects, another manifestation of the same debate. On the one hand, population geneticists like Dobzhansky and Fisher provided the experimental and theoretical bases for a reduction of organismal biology to genetics; on the other hand, the infamous exclusion of developmental biology from the MS, as well as Dobzhansky’s (1981) own research on reaction norms and gene–environment interactions in *Drosophila pseudoobscura* pointed to the limitations of straightforward reductionist approaches in biology. As is well known, a literature parallel to the MS thus originated (e.g. with the early work of Schmalhausen, 1949, and Waddington, 1942) and eventually led – among other factors – to the onset of ‘evo-devo’ as a separate field of investigation (Love, 2009), as well as to the resurgence and widespread appreciation of research on phenotypic plasticity (Pigliucci, 2001).

More recently, the genomic revolution led initially to wildly optimistic claims of what would be learned after the human genome had been sequenced (Gannett, 2008). Yet, it soon became clear that having the sequence on a CD would not straightforwardly lead to the cure of diseases or to a deep understanding of how to make a human being. Moreover, comparative genomics has quickly led to a shift in focus from what individual genes do or don’t do, to emergent complexities and systemic properties of genetic networks (Vidal, Cusick & Barabási, 2011).

Given this convoluted and controversial history, it may pay to get a bit clearer about where the concept of emergence came from and how it evolved *qua* concept (O’Connor, 2006). Perhaps the first thing to appreciate is that emergentism is usually put forth as a third way between mechanism-reductionism and vitalism-holism. Emergentists – particularly in biology – reject quasi-mystical appeals to vital forces, but at the same time argue for the appearance of genuinely novel phenomena at various levels of complexity of matter. Of course, much hinges on what ‘novel’ means in this context, as well as on the idea that there are meaningful ‘levels’ of complexity in nature. I will return to two (not mutually exclusive) interpretations of both these ideas shortly.

One of the earliest articulations of the concept of emergence in biology is due, perhaps surprisingly, to John Stuart Mill (1843: III(6)1): ‘To whatever degree we might imagine our knowledge of the properties of the several ingredients of a living body to be extended and perfected, it is certain that no mere summing up of the separate actions of those elements will ever amount to the action of the living body itself.’ The idea being expressed here is familiar in both biology and statistics nowadays: we know of plenty of examples, from chemistry and biology, where the whole – as the saying goes – is more than (or, to be more accurate, different from) the sum of its parts. Mill himself contrasted an example from physics and one from chemistry to make his point. In Newtonian physics (which was, of course, the dominant paradigm at the time), mechanical forces can be combined in an additive fashion by means of vector analysis. So, for instance, the total force being applied to a given object from two different sources is simply the sum of the individual forces thus applied. In chemistry, however, the result of a chemical reaction is pretty much never a simple sum of the reactants: we can combine, say, an acid and a base to obtain a salt (and water). The properties of the salt are in no meaningful sense simply the sum of the properties of the pre-reaction acid and base.

Arguably the next big step in the development of emergentism in philosophy of science was due to C. D. Broad (1925), who framed the issue in terms of the independence (or lack thereof) of the ‘special’ sciences (i.e. of anything that is not fundamental physics). This is very much still a topic of discussion today, usually pitting physicists on the side of one or another ‘theory of everything’ (Weinberg, 1992) and (some) philosophers who defend the notion of a fundamental disunity of science (Dupré, 1995). Broad aligned himself with the disunity camp, on the basis that he thought there are some emergent ‘trans-ordinal’ laws that are compatible with, and yet irreducible to, more fundamental principles of physics. Moreover, he did not think these laws presented any particular reason for the mystically oriented to rejoice: ‘There is nothing, so far as I can see, mysterious or unscientific about a trans-ordinal law or about the notion of ultimate characteristics of a given order. A trans-ordinal law is as good a law as any other; and, once it has been discovered, it can be used like any other to suggest experiments, to make predictions, and to give us practical control over external objects’ (Broad, 1925: 79).

It is worth sketching out the approach of two of the major modern critics of the standard reductionist programme in science, a programme that seldom appears to be questioned by many practising scientists. John Dupré (1995) has advanced the idea that the sciences are fundamentally dis-unified, which means that any talk of a 'theory of everything' is nonsense (and, in his view, even socially dangerous, because it gives priority to a particular, mechanistic, view of science and knowledge). Dupré's argument begins with the (uncontroversial, among philosophers) observation that science itself depends on metaphysical assumptions that are not justifiable empirically, and proceeds to question three related theses underlying the project of unification: determinism, essentialism, and reductionism. The first and last metaphysical positions are challenged by the idea of emergence. This is not the place for an in-depth analysis of Dupré's views (which do have their critics, e.g. Mitchell, 2003), my point simply being to note that there is a vibrant ongoing discussion in philosophy of science about issues that many scientists take for granted without further examination.

A similar example is provided by Nancy Cartwright's (1983) criticism of the unity project, this time hinging on her analysis of the concept of natural laws (her positions too, of course, have been critically evaluated, e.g. McArthur, 2006). Cartwright sees laws as empirical generalizations with more or less broad (but, crucially, not universal) domains of application. Indeed, she maintains that the empirical evidence itself strongly suggests that laws cannot be both universal and true: the only circumstances when we can verify a law of nature (say, Newtonian mechanics) to a precise extent is when we create artificial worlds characterized by highly controlled conditions. In the real world, by contrast, laws only apply given a more or less large number of *ceteris paribus* conditions. And this, of course, is the case for physics, where usually scientists take the very idea of a law of nature to be uncontroversial. In biology there are still plenty of debates – among both philosophers and biologists – about whether we can even sensibly talk about laws (as opposed, again, to mere empirical generalizations) in the first place (Mikkleson, 2003; Lange, 2005; Carroll, 2006; Elgin, 2006). While at first sight the relationship between Cartwright's views on natural laws and emergence is a bit less obvious than in Dupré's case, consider that one of the metaphysical ideas that Cartwright needs to challenge surely is reductionism, and that emergence arguably represents the major challenge for reductionist explanations of the world.

TWO TYPES OF EMERGENCE

Having briefly examined the conceptual history of emergence, it is time to make a crucial distinction between two ways of thinking about it (or about reductionism, for that matter) that have been lurking unaddressed throughout the discussion so far. One can think of emergent properties from either an ontological or an epistemological stance, although the two are not mutually exclusive. Ontology, of course, has to do with the nature of things, while epistemology has to do with how we (think we) come to have knowledge of the nature of things. Ontological claims are inherently metaphysical, while epistemological claims are not (they can be purely pragmatic, or derived from principles of logic). To complicate things further, several philosophers (though by no means all!) from the mid-20th century on began to agree that metaphysical statements ought to be evaluated in terms of our epistemic access to the world, meaning that what we can know empirically should constrain how we think metaphysically (e.g. Ladyman & Ross, 2009).

In terms of emergence and reductionism, my sense of the literature is that most philosophers nowadays are in agreement with most scientists: they reject ontological emergence and accept ontological reductionism. What this means is that the standard metaphysical position is that there are no true emergent phenomena, only phenomena that cannot currently (or even ever) be described or understood in terms of fundamental physics, and yet are, in fact, only complex manifestations of the microscopic world as understood by fundamental physics. A simple way to make sense of this idea is to deploy the concept of supervenience: in philosophy a property A is supervenient on another one, B, just in case A cannot change unless there is a change in B. For instance, if the total amount of money in my pocket is $20, this fact cannot change unless the number of coins and/or notes that make up that amount somehow diminishes or increases inside said pocket (as opposed to, say, simply exchanging a dollar bill for four 25 cent coins). Analogously, higher-order phenomena in physics or biology supervene on micro-physical phenomena just in case the only way to change the former is to change the latter (i.e. there are no genuinely emergent phenomena).

I will not comment much further on the issue of ontological emergence versus reductionism because it is of hardly any concern to the practising biologist. I will note, however, that the position I just described is rather odd, because it actually contradicts the *prima facie* empirical evidence: as Jerry Fodor (1974) famously put it, an 'immortal economist' would in vain attempt to derive the principles of his discipline from knowledge of fundamental physics. It simply cannot be done. But if our epistemology tells us that the universe behaves as if it contained genuine emergent properties (say, the properties of economic systems, which do not seem to have much to do with the properties of quarks), then is it not the case that rejection of ontological emergence is a flagrant violation of the principle that epistemology should inform metaphysics? All in all, I think the most reasonable course of action is actually to take a neutral, agnostic, stance on the matter and to proceed to where we are going next: epistemological emergence.

O'Connor (2006) helpfully describes two types of the latter, which he labels predictive and irreducible-pattern. Predictive emergence is the idea that in practice it is not possible to predict the features of a complex system in terms of its constituent parts, even if one were to know all the laws governing the behavior of said parts. Irreducible-pattern emergentists maintain that the problem is conceptual in nature, i.e. that the lower-level laws simply do not have the tools to deal with higher-level phenomena – as in the already mentioned case of Fodor's unfortunate economist with a misguided penchant for fundamental physics.

As O'Connor himself acknowledges, the distinction between predictive and irreducible-pattern views of epistemic emergence is not sharp, but it does draw attention to the fact that emergent phenomena present both pragmatic and conceptual issues for the practising scientist and aspiring reductionist. It is not just, for instance, that it would be too computationally cumbersome to develop a quantum mechanical theory of economics (the predictive issue), it is that one would not know where to start with the task of deploying the tools of quantum mechanics (indeterminacy principle, non-locality, etc.) to somehow account for the phenomena studied by economists (relation between supply and demand, boom-and-bust cycles, etc.). So, again, one does not need to be an ontological emergentist to firmly reject a greedy reductionist programme in biology or the social sciences.

TWO EXAMPLES OF EMERGENT PROPERTIES: NK NETWORKS AND G-BY-E INTERACTIONS

It will be instructive to anchor the somewhat esoteric discussion we have engaged in so far with a couple of examples from the actual biological literature, to focus our ideas about what emergence may sensibly mean in the context of biological research.

The first such example comes from a paper by Romero & Zertuche (2007) on NK networks, also known as Kauffman-type networks. Stuart Kauffman (1969) proposed these models – which are a type of cellular automaton – as an early attempt at exploring the properties of genetic networks (characterized, specifically, by N elements each with K input connections and one output). Romero & Zertuche were interested in the relationship between the properties of NK cellular automata and the robustness displayed by actual complex genetic networks in living organisms. Robustness measures the tendency of genetic networks to withstand internal disruptions (e.g. mutations) while maintaining functionality, and is related to the broader concept of evolvability (Pigliucci, 2008).

While the mathematics of Romero & Zertuche (2007) is not for the faint of heart, their results are relatively straightforward: robustness emerges from the statistical properties of a genotype–phenotype map modelled as an NK Kauffman-type network, although there are restrictions on the range of values of both N and K that yield robust mapping. Interestingly, these restrictions are within the empirical NK ranges that are derived from studies of organisms as disparate as yeast and our own species. Here, then, emergence is the appearance of a biological property (robustness) as a result of a particular type of non-linear interaction among lower-level entities (the genes in the network). Clearly, Romero & Zertuche are not making any type of ontological statement here (indeed, there is no reason they should even be concerned with ontology), but are rather deploying something like O'Connor's predictive concept of epistemic emergence. It is an open question whether research such as that of Romero & Zertuche may lead to the stronger claim of irreducible-pattern-type emergence. In this case, my hunch is that this may not be the case, as the levels of analysis – individual genes and gene networks – with which Romero & Zertuche (2007) are concerned are sufficiently close to each other to be described in terms of the same conceptual arsenal. But, again, this is an open question.

My second example is a classic one, in reference to which 'emergence' has often been brought to bear – or disparaged, depending on a researcher's metaphysical preferences: the study of gene–environment interactions (Lewontin, 1974a; Pigliucci, 2001). The debate about nature and nurture has been going on at least since Plato's idea of learning as recollection in the Phaedo, and later John Locke's (opposite) contention that the human mind is a *tabula rasa* on which experience writes out our character. In modern times, similar discussions have pitted social scientists who are inclined toward a Lockean position (think of B. F. Skinner's emphasis on operant conditioning) versus those more taken by a genetic perspective (as in *The Belle Curve* book by Herrnstein & Murray, 1994) (see Keller, 2010, for an analysis of the conceptual confusions underlying the modern version of the debate).

A better tool for thinking about gene–environment interactions has been available since the beginning of the 20th century in the form of the idea of a norm of reaction: a genotypic- and environment-specific function that displays the range of phenotypes produced by a given genotype within a given set of environments. As Lewontin (1974b) elegantly showed in reference to the specific case of the heritability of human IQ, grasping the concept of a reaction norm allows one to understand seemingly paradoxical ideas such as, for example, that a change in environmental variance may affect estimates of heritability (as it has been empirically demonstrated several times since: Pigliucci, 2001: ch. 4), even though the 'genetic' component of phenotypic variance remains unaltered.

But what does it mean to think of gene–environment interactions as 'emergent properties'? The phrase can be given at least two distinct interpretations, one statistical and pretty straightforward, the other one a bit more vague but particularly relevant to evolutionary developmental biology. Consider the statistical meaning first. In a typical reaction norm diagram one can disentangle the average effect of the environment on a given trait – measured by the mean slope of the measured reaction norms – from the average effect of genotype, measured by the mean height of the reaction norms sampled. These are both additive effects, respectively quantifiable by the so-called Environmental and Genetic (E, G) variances in a standard analysis of variance. In many cases, however, the individual (i.e. genotype-specific, as opposed to average) reaction norms are characterized by different heights in the Environment versus Phenotype space, and they also have different slopes (indicating genetic variation for phenotypic plasticity). This so-called G-by-E interaction variance is the result of (statistically) non-additive effects that cannot simply be reduced to a sum of genetic and environmental effects. A population with a significant G-by-E variance, therefore, exhibits a quantifiable 'emergent' (at the statistical, population-level) property.

There is a less straightforward, but more interesting, sense in which G-by-E represents a case of emergence in biology. As again Lewontin pointed out, if we think in terms of genetic and environmental effects as distinct causes shaping phenotypes in a more or less additive-linear fashion, we put ourselves in the naive position of trying to understand how a house is built by simply weighing the total amount of bricks and lime that goes into it. Clearly, the key to building the house lies in the specific alternating pattern in which bricks and lime interact to yield the final construction. Similarly, genes and environments continuously interact to build phenotypes throughout the process we call development. And this is a major reason why one simply cannot understand evolution without development (and vice versa), an idea that has lurked around for many decades before finally flourishing into a distinct field of evo-devo studies (Love, 2009). Of course, one thing is to appreciate Lewontin's house-building metaphor, another one is to cash out on the promise of evo-devo in order to understand the emergence of phenotypes in biological organisms. Regardless, the point remains that this – as well as the previous case of robustness – seems to represent a genuine case of emergence, at least at the epistemic level (as I mentioned above, ontological emergence is a metaphysical notion that is likely not to be settled empirically, and about which the best course of action is to maintain philosophical neutrality).

WHY EMERGENCE?

A good number of scientists are understandably wary of the notion of emergence, for the simple reason that it sounds a bit too mystical and wool-eyed. Of course, if emergence turns out to be an ontological reality, then these scientists would simply be mistaken and would have to accept a new metaphysics. However, even if emergence is only an epistemic phenomenon, there are good reasons to take it seriously, for instance because it points toward current methodological or theoretical deficiencies that make straightforward reductionist accounts unfeasible in practice, if not in principle.

Still, in order for more scientists to take emergence seriously we need a coherent account of why we see emergent phenomena to begin with. One such account has been provided recently by Brian Johnson (2010), and it is worth considering briefly. I am not suggesting that Johnson is necessarily correct, or that his explanation is the only one on the table. But it represents a good example of the contribution that philosophy of science (in this case, actually done by a scientist) can give to the way in which scientists themselves think of a given issue. Besides, Johnson may very well turn out to be exactly right.

Johnson's basic idea is simple: (at least some kinds of) emergent properties are the result of a large number of interactions among parts of a complex system, all going on simultaneously in time and space. In order to be able to grasp emergent outcomes our brains should be able to think in parallel at the conscious level (parallel unconscious thinking does occur, but it leads to an 'intuitive', not rational, grasp of phenomena). As the human brain is not capable of parallel conscious processing of information, we are faced with the impossibility of reasoning our way through the mechanics of emergence.

How do we know that the human brain cannot do parallel processing consciously? There are several reasons to think so, but Johnson provides a simple little exercise in figure 1 of his paper (Johnson, 2010) which is worth trying out to see how difficult that sort of thinking actually is, and how unsuitable we are at carrying it out. (The exercise involves summing up numbers, first on a single row – which is easy to do – then on multiple rows, which becomes immediately overwhelming.)

Interestingly, Johnson's example of an emergent property that is not mysterious, and yet that we cannot cognitively deal with, is cellular automata (for a similar take, also using cellular automata, see various works by Mark Bedau, e.g. Bedau, 2002). Johnson's (2010) figure 2 presents a standard cellular automaton, and argues that we cannot predict the behaviour of the cells in the game because our brains cannot process in parallel the various simple rules that generate such behaviour. There is no magic here, as we designed the rules and we can check – time instant by time instant – that the behaviour of the automaton is, in fact, the result of the application of such rules. But we cannot help being baffled by the complex and elegant pattern 'emerging' from the massively parallel deployment of the same rules. Analogously, there may be no mystery in, say, the emergence of robustness from the interactions going on in genetic networks, or the emergence of phenotypes during development (save, of course, for the possibility that some of these behaviours may be ontologically, not just epistemically, emergent).

If Johnson (2010) is correct, then emergence is a necessary concept to deploy across scientific disciplines for eminently practical reasons, any time that there is a mismatch in degree of complexity and interactivity between the way the world that we try to comprehend actually is and the capacities of the brains with which we try to comprehend it work. Nothing spooky or mysterious about it, just the natural result of the fact that brains that evolved to solve Pleistocene problems cannot compute in the way in which cellular automata, and countless other phenomena, ought to be computed in order to be deeply understood.

REFERENCES

Bedau M. 2002. Downward causation and the autonomy of weak emergence. *Principia* **6:** 5–50.

Bedau MA, Cleland CE. 2010. *The nature of life: classical and contemporary perspectives from philosophy and science*. Cambridge: Cambridge University Press.

Broad CD. 1925. *The mind and its place in nature*. London: Routledge & Kegan Paul.

Carroll JW. 2006. Laws of nature. *Stanford Encyclopedia of Philosophy*. Available at: http://plato.stanford.edu/archives/fall2006/entries/laws-of-nature/ (accessed 14 December 2012).

Cartwright N. 1983. *How the laws of physics lie*. Oxford: Oxford University Press.

Dawkins R. 1976. *The selfish gene*. Oxford: Oxford University Press.

Dobzhansky T. 1981. *Dobzhansky's genetics of natural populations I-XLIII*. Lewontin RC, Moore JA, Provine WB, Wallace B. New York: Columbia University Press.

Dupré J. 1995. *The disorder of things: metaphysical foundations of the disunity of science*. Cambridge, MA: Harvard University Press.

Elgin M. 2006. There may be strict empirical laws in biology, after all. *Biology and Philosophy* **21:** 119–134.

Fodor J. 1974. Special sciences (or: the disunity of science as a working hypothesis). *Synthese* **28:** 97–115.

Gannett L. 2008. The Human Genome Project. *Stanford Encyclopedia of Philosophy*. Available at: http://plato.stanford.edu/archives/win2008/entries/human-genome/ (accessed 14 December 2012).

Hendry RF, Needham P. 2007. Le Poidevin on the reduction of chemistry. *British Journal for the Philosophy of Science* **58:** 339–353.

Herrnstein RJ, Murray C. 1994. *The bell curve: intelligence and class structure in american life*. New York: Free Press.

Johnson BR. 2010. Eliminating the mystery from the concept of emergence. *Biology and Philosophy* **25:** 843–849.

Kauffman SA. 1969. Metabolic stability and epigenesis in randomly constructed genetic nets. *Journal of Theoretical Biology* **22:** 437–467.

Keller EF. 2010. *The mirage of a space between nature and nurture*. Durham, NC: Duke University Press.

Ladyman J, Ross D. 2009. *Every thing must go: metaphysics naturalized*. Oxford: Oxford University Press.

Lange M. 2005. Ecological laws: what would they be and why would they matter? *Oikos* **110:** 394–403.

Le Poidevin R. 2005. Missing elements and missing premises: a combinatorial argument for the ontological reduction of chemistry. *British Journal for the Philosophy of Science* **56:** 117–134.

Lewontin RC. 1974a. *The genetic basis of evolutionary change*. New York: Columbia University Press.

Lewontin RC. 1974b. The analysis of variance and the analysis of causes. *American Journal of Human Genetics* **26:** 400–411.

Love AC. 2009. Marine invertebrates, model organisms, and the modern synthesis: epistemic values, evo-devo, and exclusion. *Theoretical Bioscience* **128:** 19–42.

McArthur D. 2006. Contra Cartwright: structural realism, ontological pluralism and fundamentalism about laws. *Synthese* **151:** 233–255.

Mikkleson GM. 2003. Ecological kinds and ecological laws. *Philosophy of Science* **70:** 1390–1400.

Mill JS. 1843. *A system of logic*. London: Longmans, Green & Co..

Mitchell S. 2003. *Biological complexity and integrative pluralism*. Cambridge: Cambridge University Press.

O'Connor T. 2006. Emergent properties. *Stanford Encyclopedia of Philosophy*. Available at: http://plato.stanford.edu/archives/win2006/entries/properties-emergent/ (accessed 14 December 2012).

Pigliucci M. 2001. *Phenotypic plasticity. beyond nature* *and nurture*. Baltimore, MD: Johns Hopkins University Press.

Pigliucci M. 2008. Is evolvability evolvable? *Nature Reviews Genetics* **9:** 75–82.

Romero D, Zertuche F. 2007. Number of different binary functions generated by NK-Kauffman networks and the emergence of genetic robustness. *Journal of Mathematical Physics* **48:** 083506. [11 pages].

Schmalhausen II. 1949. *Factors of evolution. The theory of stabilizing selection*. Philadelphia, PA: Blakiston.

Vidal M, Cusick ME, Barabási AL. 2011. Interactome networks and human disease. *Cell* **144:** 986–998.

Waddington CH. 1942. Canalization of development and the inheritance of acquired characters. *Nature* **150:** 563–565.

Weinberg S. 1992. *Dreams of a final theory*. New York: Pantheon.