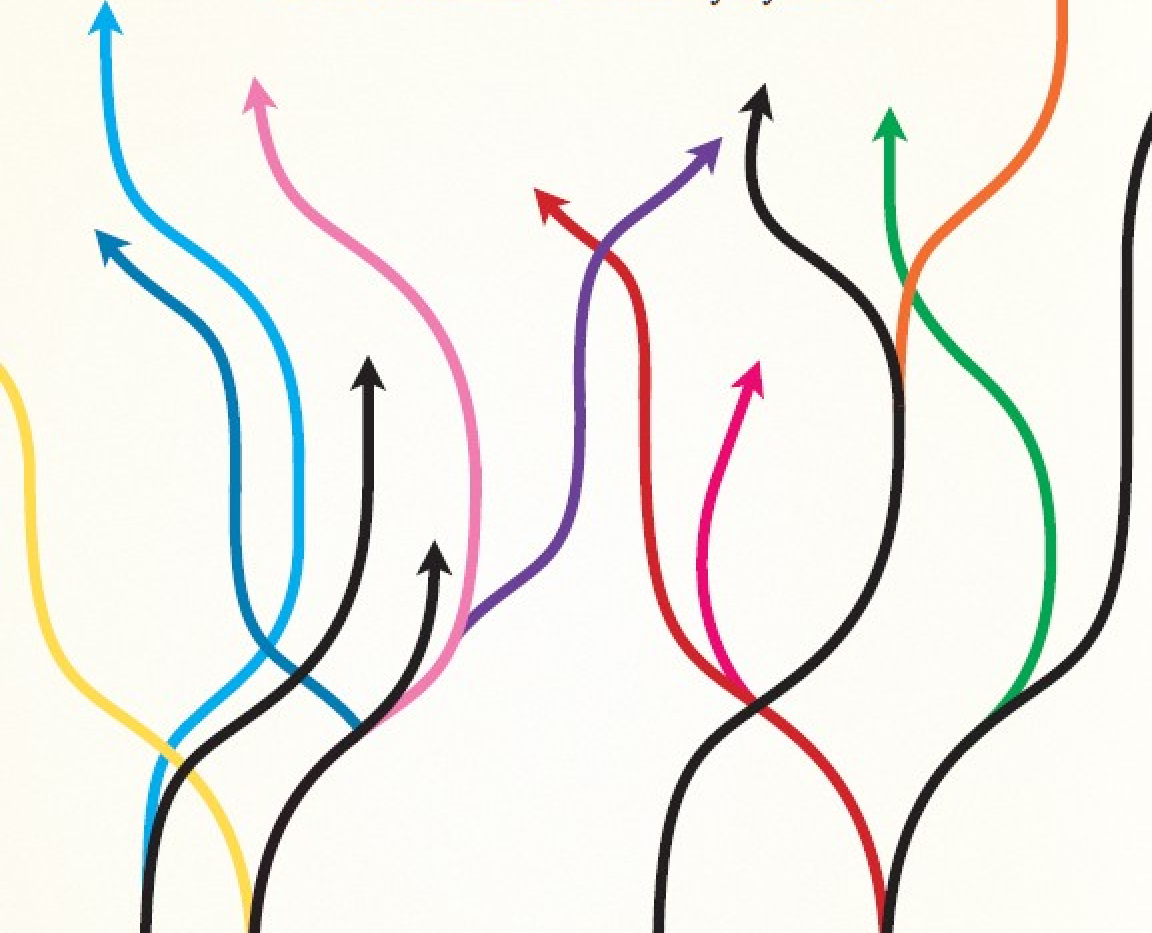
The Tendency for Diversity & Complexity to Increase in Evolutionary Systems



BIOLOGY'S FIRST LAW

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1 The Zero-Force Evolutionary Law

The history of life presents three great sources of wonder. One is adaptation, the marvelous fit between organism and environment. The other two are diversity and complexity, the huge variety of living forms today and the enormous complexity of their internal structure. Natural selection explains adaptation. But what explains diversity and complexity?

Evolutionary theory offers a number of possibilities. Diversity might be explained by natural selection favoring differentiation of closely related species, perhaps for the avoidance of competition (Darwin [1859] 1964). Or it could be the result of selection favoring groups of species with a greater propensity for speciation (Stanley 1979). The complexity of organisms could be favored on account of the selective advantages of greater division of labor among their parts (Darwin [1859] 1964). Or it could be that greater complexity means greater ecological specialization, which in turn might be generally favored by selection. Diversity and complexity could also be mutually reinforcing. As species diversity increases, niches become more complex (because niches are partly defined by existing species). The more complex niches are then filled by more complex organisms, which further increases niche complexity, and so on (Waddington 1969). There are many other possibilities, most relying on natural selection.

While there is undoubtedly much truth in these hypotheses, we argue that they are incomplete, that there exists in evolution a spontaneous tendency for diversity and complexity to increase, one that acts whether natural selection is present or not. To put it another way, rising diversity and complexity are the null expectation, the predicted outcome for evolution in the total absence of selection and other forces. They are the zero-force expectation. The reason is simply that variation arises in biological systems, and when heritable it accumulates, with the result that variances tend to increase. And both diversity and complexity are aspects of variance. Diversity in a general sense is a function of the amount of variation among individuals. And in the absence of constraints or forces, the accumulation of variation in a population will tend to increase the diversity of its component individuals. (More narrowly, diversity is number of species, of course, but speciation is just a special case in which variation becomes discontinuous.) Complexity in a general sense is a compound notion connoting an uncertain mix of multiplicity of parts, adaptation, functional sophistication, and more. Here, however, we adopt a narrower, technical understanding from biology, in which complexity is a function only of the amount of differentiation among parts within an individual. (Or in the special case in which variation is discontinuous, complexity is number of part types.) Again, in the absence of constraints or forces, the accumulation of variation in the parts of individuals in a lineage will tend to raise the variance among those parts and therefore increase the complexity of the individual.[1]

The rationale is simple. Imagine a new picket fence, in which each picket is identical to every other. With the passage of time, different accidents happen to different pickets. A pollen grain stains one. A passing animal knocks a chip of paint off another. The bottom of a third picket becomes moldy and crumbles where it touches the ground. As a result, the pickets become more different from each other. And the process continues indefinitely, so that even when the pickets are quite differentiated, further accumulation of accidents will tend to make them more different yet. In other words, the fence as a whole becomes more "complex," coming to consist of parts—pickets—that are ever more different from each other. Or from another perspective we might say the pickets become ever more "diverse." No directed forces need to be invoked here. The cause of the complexification of the fence (or equivalently the diversification of the pickets) is not gravity, electromagnetism, natural selection, or any other natural force acting on its complexity. Nor is any directed human intervention required. Rather, diversity and complexity

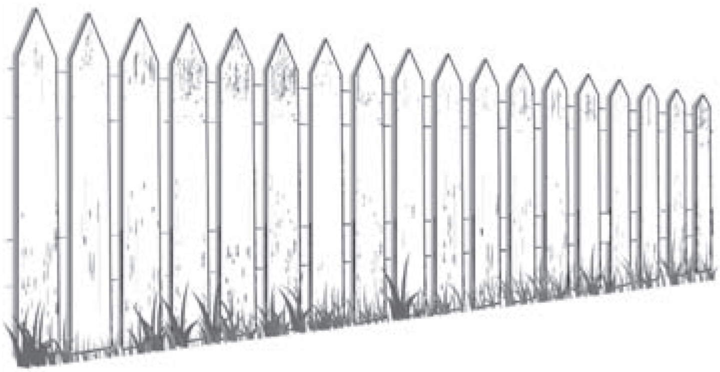

FIGURE 1

arise by the simple accumulation of accidents, producing a steady, background increasing tendency. In other words, increasing complexity and diversity is the natural state of the system, the expectation in the total absence of any forces acting on diversity or complexity.

The claim is that this same increasing tendency is the natural or background condition of evolving populations and organisms. We call the principle that governs this background condition the "zero-force evolutionary law," or ZFEL. Here is one formulation of the law:

> ZFEL (special formulation): In any evolutionary system in which there is variation and heredity, in the absence of natural selection, other forces, and constraints acting on diversity or complexity, diversity and complexity will increase on average.

The absence of constraints and forces is the special zero-force condition after which the law is named. What are these constraints and forces? Regarding forces, natural selection is far and away the best known, but we also need to accommodate the possibility that other forces may exist[2] or may someday be discovered. The special formulation of the ZFEL excludes all forces. Generally speaking, "constraints" refers to what are commonly called developmental constraints, limitations on change arising from the organization of ontogeny, as well as to historical constraints, limitations arising in evolution that are generally manifest in development. It also refers to physical and material constraints, limitations arising from the laws of nature and the properties of materials, as well as logical and mathematical constraints. In chapter 2, we state more precisely the sense in which these are excluded in the special formulation.

Notice that the special formulation does not say that diversity and complexity *will* in fact increase in every instance, only that they will increase on average. The reason is that chance could intervene. In other words, the increase is probabilistic, so that improbable combinations of events could cause diversity and complexity to fail to increase, or even to decrease. After diverging initially, the pickets in the fence could by chance become more similar to each other.

There is also a second formulation, a more general statement of the law, which does not invoke the zero-force condition:

> ZFEL (general formulation): In any evolutionary system in which there is variation and heredity, there is a tendency for diversity and complexity to increase, one that is always present but may be opposed or augmented by natural selection, other forces, or constraints acting on diversity or complexity.

What the general formulation tells us first of all is that the cause of increase in the special formulation is a tendency. It is this tendency that manifests itself as increase, on average, whenever constraints and forces are absent. Second, it says that this tendency is to be understood as present even when constraints and forces do act. For example, the tendency could be blocked by constraints, or opposed and even overcome by selection, with the result that diversity or complexity does not in fact increase, even on average. Or selection could oppose the tendency strongly enough to overwhelm it, so that diversity or complexity actually decreases. The general formulation says that, when these contrary forces or constraints act, it is not because the ZFEL tendency has vanished. Rather, the tendency remains and continues to act even while constraints or forces are overcoming or overwhelming it. Analogously, the picket fence may not actually become more complex, if someone is regularly fixing and painting it. But the complexification tendency is understood to be present and acting anyway, continuously, even while the repair process is going on.

Finally, the general formulation allows that forces or constraints may also favor diversity or complexity, augmenting the ZFEL tendency. Diversity or complexity increases more than it would if either the ZFEL tendency or the augmenting constraint or force were absent. In sum, the ZFEL tendency is to be understood as a background state that is present prior to and during the imposition of any constraints or forces. In this view, the effect of any imposed constraint or force is always the resultant of two factors, one of which is the ZFEL.[3]

A Unification

We do not consider the ZFEL a new discovery. All it really says is that there is a tendency for variation to arise and to accumulate, and that it will do so unless opposed in some way. And some such principle has been part of the implicit working knowledge of every evolutionist since Darwin. Further, many applications of the principle have long been known and appreciated in biology. For example, it is known that, in the absence of selection, a population tends to diversify as a result of mutation, recombination, and random mating (Gould and Lewontin 1979). At the molecular level, a spontaneous diversifying tendency is implicit in the methods used to isolate the effect of selection from drift (Kreitman 2000; Yang and Bielawski 2000; Bamshad and Wooding 2003). And the ZFEL is clearly central in recent work on gene duplication and divergence, especially the work of Lynch (2007b; also Ohno 1970; Taylor and Raes 2004).[4] At a larger scale, an expectation of divergence is present in standard phylogenetic models that treat species as particles and their evolution as a Markov process (Raup et al. 1973). The principle arises too in null models of the evolution of phenotypic diversity (also known as "disparity"), which predict that physical differences among species tend to increase (Foote 1996; Gavrilets 1999; Ciampaglio, Kemp, and McShea 2001; Pie and Weitz 2005; Erwin 2007). For complexity, the principle underlies the notion of duplication and differentiation of parts (Gregory 1934, 1935), including genes, considered as parts. And it is traceable historically to Herbert Spencer's (1900) notion of the "instability of the homogeneous." Spencer argued that the parts of individuals in a lineage should tend to become more different from each other as they accumulate heritable accidents.

What is new, what the ZFEL offers, is a recognition of the unity among these cases, of the common thread that runs through standard thinking about them. The ZFEL makes the common principle explicit and gives it a name. The ZFEL also turns out to have real consequences for research. It is testable, and as we will argue later, it opens new research avenues. In particular, it reconfigures the long-standing problem of the origin of and rise in organismal complexity. As we will see in chapters 5 and 7, it suggests that the real puzzle in evolution is not why organisms are so complex but why they are not more so.

More generally, what the ZFEL offers is a gestalt shift for evolutionary biology, a radical change in our view of what is pattern, and therefore needs special explanation, and what is background. In the standard view of evolution, increases in most variables are understood to require a force, such as natural selection. In the ZFEL view, increase is the background condition, with natural selection in the role of superimposed force, augmenting or opposing the background increase.

A Newtonian Analogy

We propose that the role the ZFEL plays in evolutionary theory is analogous to inertia in Newton's first law. Inertia—lack of change—is the default, or "natural," state of velocity, the background against which gravity and other special forces act. The first law says that, if no force acts on an object, its velocity will remain constant. It is deviations from constant velocity that require forces. Analogously for diversity and complexity in biology, it is deviations from the increase predicted by the ZFEL that require forces. Paradoxically, our familiarity with Newton's laws makes the claim here somewhat counterintuitive. As Newtonians, we are comfortable with the idea of constancy as the null expectation. (That is, constancy of velocity, of course, not constancy of position, unless velocity is zero.) Indeed, so deeply ingrained is the Newtonian paradigm that we sometimes accept the following as a gloss of Newton's first law: if no force, then no change. In contrast, the ZFEL says that, in evolution, the expectation in the absence of any forces is change. If no force, then change.

A Law of Evolution

We have chosen to call the zero-force principle a law for two reasons. First, it is true everywhere and always, in all evolutionary systems with variation and heredity. That is, it applies equally to all evolutionary systems on Earth, past and present, and to all evolutionary systems that may exist, or may have existed, elsewhere. If, as Darwin said, "natural selection is daily and hourly scrutinising, throughout the world, every variation" (Darwin [1859] 1964, 84), then the ZFEL is daily and hourly tending to increase variation, throughout this and all other life-bearing worlds. It is universal, we claim. Second, the ZFEL is not analytic. It is not true as a matter of logic or mathematics, as is biology's so-called Hardy-Weinberg law. Rather, it is synthetic, making an empirical claim about the way the world is. The world could in principle have been otherwise. However, the law is different from most other synthetic generalizations in biology that have been called laws, such as Mendel's law of independent assortment (alleles for different characters segregate independently), and different too from any of the many "rules" that are sometimes called laws, such as Cope's rule (that body size increases on average). The ZFEL is not an empirical generalization that arises from other contingent facts of biology or from observation of the pervasiveness of some phenomenon. We have not examined the data on diversity and complexity over the history of life and discovered there an increasing tendency.[5] Rather, the ZFEL arises from the contingent properties of variation in nature, properties that are the formal domain of probability theory. (See chapter 6.)

Law and a Gestalt Shift

The two main points of the last few sections are worth a summary restatement. We are proposing both a new law and a gestalt shift. The law is a universal tendency for diversity and complexity to increase. And the gestalt shift places this tendency in the background, moving the effect of natural selection and various constraints on diversity and complexity to the foreground. Our experience is that those who pay attention to the law but overlook the gestalt shift are sometimes confused by our claims. In particular, they may imagine we are claiming that diversity and complexity *must* increase and that the ZFEL is the cause whenever it does, claims that are instantly refuted by the many instances of decrease known from the history of life and the many cases of diversity and complexity increase known to have other causes, such as selection. In fact, however, what we claim to have identified is a background tendency, one that acts everywhere and always but that may be overcome at any turn by foreground forces (such as selection) and constraints. To help the reader keep the structure of the argument in mind, we recall it, using various analogies, throughout the book—we hope not so often as to test the reader's patience.

Diversity and Complexity

Our usage of "diversity" is conventional, but that of "complexity" is not. Here "complexity" just means number of part types or degree of differentiation among parts (McShea 1996). This choice will sound odd because in colloquial usage complexity means so much more, connoting not just part types but functionality, sophistication, and integration, among other things. We call complexity in the parts-and-differentiation sense "pure complexity," to distinguish it from the much broader "colloquial complexity." Some will find the notion of pure complexity disconcerting on account of the severing of any connection with function and natural selection. The central questions in biology have centered on function, on what the parts of an organism are *for,* and how they interact to enable the organism to *do* things, behaviorally or physiologically. But in our usage, even functionless, useless, part types contribute to complexity. Even maladaptive differentiation is pure complexity. We understand the objection. And we have two answers to it. First, we agree that function is important. But this book is about something else. The questions we raise have to do with "How many?" rather than "What for?" They have to do with "How differentiated?" in a sense that is independent of "How capable?" In effect, what pure complexity does is enable us to ask the same questions about organismal structure that diversity lets us ask about ecological structure. Diversity too is a "how many" concept. How many types of individuals? How many different species? To ask these "how many" questions about diversity and complexity, definitional independence from function is essential.

Second, a notion of pure complexity, independent of function, is essential precisely so that one can ultimately address the relationship between complexity and function, between complexity and natural selection. One could not, for example, ask whether complexity is favored by natural selection, whether complex structures are more functional than simpler ones, on average, if one's notion of complexity had the effects of natural selection—that is, function—built into it. In investigating a relationship between *A* and *B,* it is helpful, to say the least, to define *A* and *B* so that they are conceptually independent of each other. We discuss this further in chapter 4.

A consequence of our use of a function-free notion of complexity is that there will initially be little connection between what we are talking about and "complexity" as it has been used in most of the evolutionary literature. Peppered throughout that literature are references to "organized complexity" and "adaptive complexity," as well as to the "information content" and the "computational power" of organisms, with an assumed connection between information or computation and complexity in some sense. Often these terms arise in discussions of what is taken to be an obvious directionality in evolution, sometimes called "evolutionary progress," the rise in "complexity" from bacterium to human. The concern in this literature is clearly with complexity in the colloquial sense, and we will return to colloquial complexity or something like it (in chapter 7) in order to say something about how it might arise in evolution. But, as we hope will emerge, understanding its poorer cousin, pure complexity, is a necessary first step. In the meantime, we ask readers to hold in suspense everything they think they know about complexity in biology, including its possible increase in evolution. We will be offering a new view in which the colloquial notion and the possible trend emerge in a new light.

It is also worth mentioning here at the outset that our treatment shares the word "complexity" with a field called "complex systems," a hot area in the past twenty years. Complex systems are usually taken to include not only organisms but also markets, technologies, social and political organizations, many-body physical systems, and computer programs with problem-solving abilities like cellular automata, NK networks, and neural nets. We want to be clear here that our understanding of complexity is different, and that there is no connection between our project and these various complex-systems research programs, at least no direct connection.[6] Complexity in our sense, pure complexity, is not a function of the nonlinearity of interactions in a system, the sophistication of a system, or a system's ability to survive, reproduce, adapt, compute, or think. Pure complexity is not connectedness or integration. It is not the length of the shortest description of a system or of the algorithm for generating it. It has nothing to do with the amount of energy a system uses or how it uses it. In this book, the phrase "pure complexity," or just "complexity" alone and unmodified, always means number of part types or differentiation among parts. And nothing more.

Hierarchy

In the chapters that follow, hierarchy will emerge as central in our understanding of the ZFEL. We understand hierarchy in the sense of physical nestedness.[7] Higher levels are composed of lower-level parts. Aggregates of lower-level units physically constitute higher-level entities. As a preview of the role of hierarchy, consider these two points. First, the ZFEL applies at all levels where there is heritable variation. It predicts increase in diversity and complexity of genes, macromolecules, organelles, cells, tissues, organs, individuals, groups, populations, species, clades, or higher-level units.[8] Second, the ZFEL applies to each independently. Indeed, in principle, the ZFEL could manifest itself differently at each level. This is an important point. As we will see, measures of complexity and diversity are level relative. For instance, organismic complexity might be measured in terms of differentiation among cells or, in the discrete case, number of cell types. But cellular complexity might be measured as the number of types of cell structures, organelles, and such. Thus, it is perfectly coherent to say, for example, that in evolution, multicellular organisms became more complex (more cell types) while their component cells became simpler (losing certain cell structures, perhaps favored by selection for specialization) (McShea 2002). Similar remarks could be made about diversity. A clade might become more diverse (more species) even while its component species decreased in diversity (less variation within each species). Given all this, our hierarchical approach is not just convenient, it is necessary. No single-level account, no reductionistic account, could capture the phenomena. Thus, in our hierarchical view, the genetic or macromolecular level—deemed conventionally to be central to understanding evolution—is just one among many and is not privileged in any way. As a consequence of our apostasy on this matter, genes and macromolecules, although discussed in what follows, are not mentioned explicitly in the ZFEL and are not central.

Diversity Is Complexity, Complexity Is Diversity

Diversity and complexity might seem like an odd pair. In conventional usage, one is a much-studied and well-understood property of populations or taxa, and the other is a poorly studied and barely understood property of organisms. So it might seem strange that the same principle would apply to both. The explanation is simply that both diversity and complexity are aspects of variance. As mentioned earlier, diversity can be understood either in its continuous sense, as degree of differentiation among organisms or taxa, or in its discrete sense, as number of types of organisms or taxa (e.g., number of species). In either case, it is a function of the amount of variation among organisms. Pure complexity—whether understood as degree of differentiation among parts or as number of part types—is likewise a variance concept. It is variance among parts within an organism rather than among organisms. Thus, the ZFEL says that variation occurs, and in systems with inheritance it tends to accumulate, with the result that variance increases. And it will do so whether the system consists of a set of organisms or a set of parts within an organism.

But the relationship between diversity and pure complexity is closer than that. They are really one and the same thing, considered from hierarchically adjacent vantage points. That is, the diversity of a system at level N is just its complexity at level $N + 1$. For instance, diversity at the cellular level = complexity at the organismic level. An organism with a great diversity of cell types is a complex organism. Moving up a level, diversity at the organismic level = complexity at the group level. A group of organisms that is diverse can be said to be a complex group. This last is not ordinary usage of the term "complex," of course, and it will sound odd to most biologists.[9] But that is because most think of complexity as a compound notion implying both number of part types and functional organization. However, recall that in our technical treatment here, we are considering only the function-free aspect of complexity, pure complexity (see chapter 4). Thus, the identity between complexity and diversity follows.

In the following chapters, we consider diversity and complexity separately because they have been treated separately in the literature, and different issues have grown up around them. So the ZFEL needs to be framed differently for each of them. However, as we hope will be clear, the argument is essentially the same for both.

Diversity and Complexity, Not Adaptation

It should be obvious already that this treatment differs from the vast majority of empirical and philosophical works in biology in that the mission is *not* to understand the origin and evolution of adaptation. Our concern is with diversity and complexity, which natural selection can act upon but which, we claim, are also subject to a tendency independent of selection. We have done, and will do, everything in our power to convince readers that we are serious about this unusual focus. But given the adaptationist bent of biology since Darwin and the power of traditional formulations to straitjacket thinking, we expect that some will occasionally find themselves confused about the nature of our project. To these readers, we first apologize for the limitations of our rhetorical skills. And second we encourage them, when faced with apparent incongruity, to rethink what we are saying with our special focus in mind: the ZFEL is about a particular property of biological entities, the amount of variation in them, and how the amount of variation is expected to change in evolution. As will be seen, the ZFEL has consequences for adaptation. But it is not a claim about adaptation. Returning to our analogy with inertia and Newton's first law, our claim is that just as the Newtonian needs the First Law to understand the effects of special Newtonian forces, so the evolutionary biologist needs an understanding of the ZFEL before investigating adaptive evolution.

The ZFEL and the Second Law of Thermodynamics

Based on what we have said so far, some will be poised and ready to make a leap, from the notion of accumulation of accidents to the second law of thermodynamics (Pringle 1951; Brooks and Wiley 1988; Collier 1986, 2003). We advise readers against this, for their own safety. We are concerned that on the other side of that leap there may be no firm footing. Indeed, there may be an abyss. First, we think the foundation of the ZFEL lies in probability theory, not in the second law or any other law of physics. And second, our notions of diversity and complexity differ fundamentally from entropy, in that entropy, unlike diversity and complexity, is not a level-relative concept. (We explain these claims further in chapter 6.) Still, some work in recent decades on the application of the second law to biology has been inspirational (especially Wicken 1987; Brooks and Wiley 1988; Salthe 1993), and we gratefully acknowledge the intellectual debt.

Outline of the Book

Chapter 2 explains our understanding of randomness, as it relates to the ZFEL, and addresses the in-principle problem of how random processes can create a directional tendency. It also explains how we are thinking about hierarchy and constraint. Chapter 3 explains how we are using the term "diversity" and how the ZFEL applies to diversity. Chapter 4 does this for "complexity," giving an extended discussion of our choice of this word and explaining our understanding of the notion of a "part." In each of these two chapters, we offer a key piece of the evidence that supports the ZFEL, and then chapter 5 reviews the evidence more broadly. Chapter 6 treats certain philosophical issues that arise, including a possible theoretical foundation for the ZFEL. And chapter 7 discusses some of the implications of the ZFEL for biology.

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