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978-1-108-71668-0 — The Missing Two-Thirds of Evolutionary Theory
Robert Brandon , Daniel W. McShea
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1 Introduction

Adaptation, diversity, and complexity – the three signature concepts of evolution, the three drivers of evolutionary research, the three great mysteries of life on Earth. Everyone knows they are distinct, but we are prone to blurring the distinctions, to assuming a close association among them, empirically and even conceptually. If something is diverse or complex, it must also be adapted, and vice versa.

The empirical separation is obvious and easy to demonstrate. Hugely expanded forebrains are adapted and complex, but the hominids that have them are not especially diverse. Red blood cells are diverse among vertebrates and well adapted for carrying oxygen, but these cells are not complex. The dinosaurs were diverse, with anatomy and physiology as complex as any animal's, but in the end they were not very well adapted (at least, not adapted enough to survive the late Cretaceous bolide impact).

Less obviously, there are conceptual separations that we often need to be reminded of, between adaptation on the one hand and diversity and complexity on the other. First, they are not just distinct; they are incommensurate. Adaptation is a relationship between an organism and its environment. An adapted organism is one that is likely to produce many offspring in that environment. Diversity and complexity are not relationships of any kind. They are absolute measures. They are numbers. Diversity is number of taxa (or, as we discuss later, degree of differentiation among taxa). Complexity is number of part types (or degree of differentiation among parts).

Second, adaptation on the one hand and diversity and complexity on the other are not even concepts of the same order. Adaptation is what one might call a first-order concept, like size, with each entity having some value attached to it. In contrast, diversity and complexity are second-order concepts. They apply only to groups or sets of entities. Diversity refers to differences within a group of organisms, species, or higher taxa. Complexity is differences among a set of parts within an organism. Diversity and complexity are variance concepts.

For adaptation, the body of theory that has been built up since Darwin is huge and robust. And nothing we have to say in this Element challenges a single principle or core claim of that body of theory, at least none that have been articulated. Our treatment is Darwinian, through and through. On the other hand, we do challenge one of the reflexes, the tics, of contemporary Darwinism, the very un-Darwinian tendency to assume that natural selection, and natural selection alone, governs all of evolution. Stephen Jay Gould and Richard Lewontin's (1979) famous Spandrels paper savaging this tendency had a salutary effect for evolutionary thinking in general, but it was less effective for diversity and complexity in particular. For these

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two, the common reflex assumption is still that selection rules. In fact, as we have shown in our earlier book and hope to amplify in this Element, selection is one of two important factors governing diversity and complexity. The other is the zero-force evolutionary law (ZFEL). The ZFEL is not inconsistent with Darwinian theory. Indeed, as we will show, the underlying principle is implicit in that theory. But theory routinely ignores it. The error, if we choose to call it that, lies in the application of Darwinian theory to diversity and complexity, seeing adaptation as sufficient when it is not. Thus, for contemporary Darwinian theory and its treatment of diversity and complexity, our summary statement is this: good theory, bad application.

We need to say a few words about the title, about the phrase "missing two-thirds." Evolutionary thought has a general theory of adaptation, a principle – natural selection – that explains adaptation wherever and whenever it occurs. Our claim is that what is "missing" is a general theory of diversity and complexity. Now there has certainly been a great deal of empirical work on diversity, at all scales, from the very recent and rapid human-driven global decline to the comparatively slow and fitful rise of diversity over the history of life. There has been much less but still *some* empirical work on the trajectory of complexity. And there has been much theorizing about the factors at work in particular historical episodes of change in diversity, such as the Cambrian explosion and the Permian and late Cretaceous mass extinctions. Again, there has been less for complexity, although the rise of metazoan complexity in the Cambrian has attracted some attention. But there has been no general theory, no set of principles laid out, that either explains or lays the foundation for explaining *all* change in diversity and complexity, wherever and whenever it occurs, nothing like what we have for adaptation. Our first book, in which we offered a qualitative formulation of the ZFEL, was an attempt to develop such a theory. In this Element, we extend that treatment a step further, offering a theory of diversity and complexity, one that is not only general but quantitative.

What about the "two-thirds"? Having said that there are three concepts, we may now have to backtrack a bit. In standard usage, *diversity* and *complexity* are different. *Complexity* is within-organism variance. *Diversity* is among-individual or among-taxon variance. And from that perspective, they make up two-thirds of the grand trio – adaptation, diversity, and complexity. But one could also see diversity and complexity as the same concept, variance, applied at different levels of the biological hierarchy. In that case, it would be more accurate to say that only half of evolutionary theory is missing (which in a way would be a relief, making the void seem less frightening). But whether two-thirds or a half, the gap strikes us as serious. If modern theory has not been blinded by its selectionist impulses, it has certainly been blinkered by them, glimpsing the factors underlying diversity and complexity only incompletely and fleetingly. Here, as in our first book, our hope is to bring them forward, to position them in the center of theory's visual field, where they cannot help but be noticed.

Section 2 presents what we call the zero-force evolutionary law. In this section we give a qualitative version of the law, which is what we developed in our earlier book (McShea and Brandon 2010). Just what it means and why it is true are explained. Having said what the ZFEL is, in Section 3 we briefly say what it is not. In particular, we cover what we think have been the most prevalent misunderstandings of our earlier work. Section 4 gives two different, but closely related, quantifications of the ZFEL. Quantification of the ZFEL has two main virtues. First, it offers a clear mathematical demonstration of the basic claim underlying the ZFEL, namely, that two independently evolving entities will tend to diverge. This claim is counterintuitive (since two random walks should converge as often as they diverge), but our mathematical models prove it to be true and, furthermore, help educate our faulty intuitions about pairs of random walks. Second, a quantified ZFEL is able to play a special role in a zero-force theoretical framework, analogous to the role of Newton's first law in physics. If we can quantify just how much two lineages should diverge, then we can say with some quantitative precision what forces need to be invoked when observations fall outside of ZFEL-based expectations.

That is all abstract theory. The implications of this for biology are discussed in Section 5. Having developed the theory necessary for testing the role of selection in the evolution of diversity and complexity, we could stop and wait for the evidence from numerous studies of particular cases of diversity or complexity to build up. That is the epistemologically cautious thing to do, and we do approve of that attitude. But we also think that we know enough to make some educated guesses. We come to somewhat different conclusions with respect to diversity on the one hand and complexity on the other. The ZFEL has certainly pushed complexity forward in evolution, but we cannot account for the actual trajectories of the evolution of complexity without invoking pretty consistent selection against complexity. In contrast, there are good reasons to think that the diversity of life at the largest scale – globally, on timescales of hundreds of millions of years – is governed *mostly* by the ZFEL. The claim arises from a combination of the theory and some simple facts about biology. It is an empirical claim, one that can in principle be checked using the quantitative formulation. This pair of conclusions may seem odd, since we have argued that diversity and complexity are one and the same thing but viewed from adjacent hierarchical levels. We show that, however odd, it is consistent and, beyond that, quite likely.

2 The Zero-Force Evolutionary Law

2.1 Zero-Force Laws

Aristotle and Newton looked at the physical world in radically different ways. And the word *radical* in the previous sentence almost certainly understates the case. It is hard for scientifically literate people living in the twenty-first century to fully appreciate the fundamental differences in conceptual frameworks used by Aristotle and Newton. For Aristotle, the natural state of physical objects is rest. Motion (whether accelerative or not) requires the imposition of a force. In contrast, for Newton, the natural state of physical objects is constant velocity (with $v = 0$, i.e., rest, counting as constant velocity). Living on the face of Earth, with its viscous atmosphere, it is hard to see who is right. Sitting in an armchair, as philosophers are wont to do, every visible thing is at rest. This fact fits Newtonian and Aristotelian physics equally well. (For Aristotle, these objects – pen, notepad, laptop, etc. – are in their natural state; for Newton, they are moving with constant velocity equal to 0.) Looking out the window, where right now there happens to be a hurricane blowing, leaves, branches, and the occasional small animal are flying past. Aristotle would claim, and he would be right, that these flying objects depend on a constant force being imposed upon them. Of course, Newton agrees, because he would see this case as one where the viscosity of the air produced a backward directed force on the objects that the forward directed force of the wind must overcome.

We want to draw two points from this. First, settling on the correct view of the natural state of motion, or the correct zero-force law, is not a straightforward empirical issue. Newton's first law is not a statistical generalization. (See Nabi 1981 for a hilarious spoof of what physics would look like if the laws of motion were decided by statistical methods.) Rather, the issue between Aristotle and Newton is theoretical – which theoretical framework works best in doing physics? With the benefit of hindsight, we can say that the move to the Newtonian framework was a great advance for physics. The second point has to do with the advantages of a quantitative theoretical framework. Aristotle had nothing close to a quantitative theory of physics. Newton's physics was quantitative, so that he could, for instance, go beyond the qualitative statement that the force of aerodynamic drag works in the opposite direction of the force of the wind operating on the squirrel that just blew past. These forces can be assigned quantities so that we can make quantitative predictions about direction, velocity, and acceleration of the squirrel.

In particular, when we know the quantitative value of one force, we can deduce the quantity of the second opposed force, but only in the context of a zero-force law. For instance, near the surface of the Earth, we know the quantity of the gravitational force acting on a falling object, and so we can deduce the force of drag from Newton's first and second laws (the second law being $F = ma$). More generally, any quantitatively characterized deviation from inertial motion (described in the first law) tells us the quantity of the net force acting on the system. This is our goal for the ZFEL: describe the zero-force condition for diversity and complexity and then use that in conjunction with observations to deduce net forces, such a natural selection. Immodestly put, we aim to do for biology what Newton did for physics.

One important consequence of this needs emphasis. In statistical sciences, there is an important distinction between two methodologies. One is null-model testing, where one sees whether observations are, or are not, significantly different from what the null model predicts. There are only two possible conclusions from such a test: either we reject the null (but are given nothing in its stead) or we do not reject the null (which, of course, does not mean we should accept the null). If one's goal is to find some hypothesis that is reasonable to believe, then this methodology is not adequate. A second methodology can deliver reasonable beliefs, namely, the methodology of maximum likelihood testing. Here we compare two or more hypotheses to the data. Each hypothesis has a likelihood given the data, and this methodology tells us to accept the one that has the highest likelihood. Null-model testing is great for those wishing to avoid false beliefs, and maximum likelihood is great for those wishing to maximize their true beliefs. There is no accounting for matters of epistemological taste.

Null-model testing within the context of a zero-force theory has all the epistemological virtues of null-model testing more generally, as discussed above. But it also delivers an alternative hypothesis when the null is rejected. Consider Newtonian physics. When a massive object is observed to be accelerating, we reject the Newtonian null of no acceleration, but we are then immediately given a (quantitative) hypothesis of the net force acting on the object. It is true that we are not given the nature of this net force – we are not told whether it is gravity or electro-magnetism or something else – but we are given the direction and magnitude of this net force. A zero-force theoretical structure gives us a way to have our epistemological cake while eating it. One might be disappointed in the cake, that is, one might be disappointed that the hypothesis delivered does not specify the nature of the force, but even this is oftentimes mitigated. For instance, in the physics of planet-sized objects, we can usually hone in on gravity. And in biology, we can often implicate selection. Here is the short version of this Element: don't take selection as your default hypothesis; only invoke selection when stochastic behavior of independently evolving

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entities (the ZFEL) has already been factored in and there is some remainder left to be explained.

2.2 The Principle Underlying the ZFEL

The ZFEL says that in the absence of imposed forces and constraints, diversity and complexity tend spontaneously to increase. The reason is that variation accumulates, with the result that entities tend to become different from each other, to diverge. When these entities are organisms or taxa, this divergence is an increase in variance and therefore an increase in diversity. When the entities are parts of organisms, the divergence is an increase in complexity.

The principle is simple and familiar to everyone, at least in nonbiological contexts. A group of cars that are essentially identical the moment they come off the assembly line will be treated differently, suffer different accidents, and, as a result, look very different from each other years later. They diverge. The variance in form among them increases. A group of kindergarteners released onto a playground at recess time tends to spread out, to disperse throughout the playground with time. The variance in their locations increases. Daughter languages diverge from the parent language and from each other over time. The variance among them in spelling, usage, idioms – in every feature of a language – tends to rise. They diverge.

The principle is familiar, as we say, but its application to the structure of organisms (complexity) and the structure of taxa (diversity) is not straightforward. In this section, we try to explain exactly how it can be done.

2.3 The ZFEL

Here is the formal statement of ZFEL, from McShea and Brandon (2010):

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

We called it a "special formulation," because it applies in, but not only in, the special case where forces and constraints are entirely absent. Notice that the phrasing parallels Newton's first law, describing the behavior of objects in the absence of forces. The ZFEL says that in the absence of forces, diversity and complexity increase, on average. Newton's first law says that in the absence of forces, objects travel with constant velocity. Both this formulation of the ZFEL and Newton's first law are in-principle statements, designed to tell us what happens when nothing happens (i.e., when no forces impinge on the system).

But we hasten to emphasize the fact that the special formulation of the ZFEL does indeed apply to cases beyond the ideal case of no forces and no constraints. That is good, because as we point out below, the case of no constraints is a conceptual impossibility. In contrast, the case of no selection is conceptually possible, though perhaps empirically rare. However, the special formulation above does not have such a limited application. Notice it describes the absence of forces or constraints acting on diversity or complexity. Consider an example of two lineages, A and B, and a trait, mean height, that differs between them. (This is a diversity example, for a complexity example take A and B to be two parts of a common whole, e.g., two vertebrae in a mouse.) The special formulation of the ZFEL applies when selection acts on some other uncorrelated trait, say, color. In that case, a force is present, but it is not acting on the trait in question, height. The special formulation also applies when selection acts directionally on height in both lineages, provided it does so in each lineage independently, that is, provided it is not directly favoring the two lineages becoming more similar or directly favoring their become more different. Thus when selection acts independently on each lineage, a force is present, but it is not acting directly on diversity. In sum, the special formulation *does not* apply to cases where selection acts directly on diversity. That is what the absence-of-force clause in the special formulation rules out.

Thus, whether the special formulation of the ZFEL has a wide or narrow range of application is an empirical matter, one that cannot be settled by the bromide that selection and constraints are always present.

So to cover a broader range of cases, we also gave a general formulation:

> 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.

The critical word in this formulation is “tendency.” When forces or constraints are present, diversity and complexity have a tendency to increase. A tendency is a kind of push or straining toward increase. It is not an actual outcome. In other words, the general formulation of the ZFEL does not say that diversity and complexity *will* increase, only that there is a kind of pressure, or oomph, toward increase. Analogously, if I lean against my house, I impart to the house a tendency to fall down. The house does not fall down, indeed it does not even come close to falling down, because my leaning is resisted by various forces and constraints, but the tendency is there nonetheless, so long as I am leaning against it. In the same way, the ZFEL says that lineages and parts have a tendency to diverge from each other, even if – owing to selection and constraints – they do not diverge. The implication of course is that the moment those forces and constraints are removed, divergence would begin.

Our usage of the word tendency is conventional, but we note that occasionally, in some contexts, the word is also used to describe an actual trend. One hears it said that the stock market has shown an upward tendency over the past year, meaning simply that some indicator has increased, that there has been a trend In our understanding, however, the fact of the trend by itself gives no information about a tendency. There could have been an increasing tendency, imparted perhaps by market forces, but the trend could also have been due entirely to chance, with no underlying upward tendency. In any case, here, for the ZFEL, a tendency is a kind of predisposition to increase, not a result, not an actual trend. We say more about this shortly.

2.4 A Simple Model

The model in Figure 1A shows why the ZFEL works. When forces and constraints are absent, evolving entities – lineages (for diversity) and parts (for complexity) – change randomly, and as a result they diverge from each other, on average. The figure shows a group of 10 entities, changing in a size morphospace. As shown, they all start at the same size, 20 mm. For complexity, the figure might represent 10 teeth in a reptile's tooth row, all initially 20 mm long. For diversity, it might represent body length in a population of 10 individuals of some insect species, all 20 mm long.

In the model, each entity changes randomly, increasing or decreasing in length by 1mm in each time step, always with 50:50 probability. The result is 10 random walks, shown over 30 time steps. Notice that at the end of 30 time steps, the random walks have dispersed considerably. The histogram above the trajectories shows what the expected distribution would be if there had been hundreds of random walks, rather than just 10. The Central Limit Theorem tells us that the histogram approximates a normal distribution, with variance equal to the number of time steps. Thus diversity or complexity – here measured as the variance –increases without limit. In other words, the ZFEL expectation is not only that diversity and complexity increase initially, when lineages or parts are quite similar to each other, but also later, when they have become quite different. Even for a diverse set of individuals or species, the ZFEL expectation – in the absence of forces or constraints – is even greater diversity. And for individuals that are already quite complex, having highly differentiated parts, the expectation is even greater complexity. Of course, the expectation is probabilistic. In any time step, diversity or complexity may decrease, if by chance

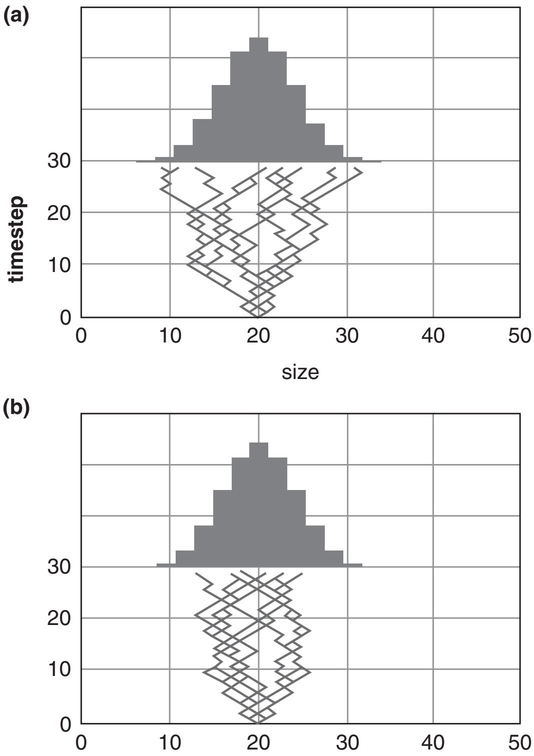

Figure 1 (A) Special formulation of the ZFEL. Ten entities following independent random walks over 30 time steps. The histogram shows the distribution of outcomes for a much larger number of random walks. (B) General formulation of the ZFEL. Trajectories of the 10 entities are limited by selection and constraints (see text), but the *tendency* to spread is present the entire time. (The histogram from A – the expectation due to the ZFEL – is copied here to enable a comparison of the actual with the expected.)

entities vary in such a way as to become more similar to each other. But the expectation, the on-average result, is always increase.

No absolute timescale needs to be specified here. What we call *time steps* can be thought of as generations, or million-year increments, or even longer units of time. The ZFEL principle operates on all timescales. Also, here and in what follows, the horizontal axis is treated as an additive scale, but recognizing that changes in biology tend to be proportional, one could instead interpret it as a log scale, with increases and decreases occurring in units of constant proportion.

Figure 1A illustrates the special formulation of the ZFEL, showing divergence when selection and constraint are absent. Figure 1B shows one way that

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the general formulation of the ZFEL could become relevant. Suppose the evolving entities are 10 teeth in a tooth row and that selection opposes any decrease in tooth size below about 15mm, perhaps because a smaller tooth is unable to apply enough force to properly pierce an important food, say, a hard seed. Also suppose that a developmental constraint imposed by jaw size limits tooth size to a maximum of about 25mm. In this version of the model, teeth still change randomly, and divergence still occurs, driving complexity initially upward, but divergence is eventually limited by selection below and constraint above. As a result, the divergence histogram from Figure 1A, reproduced in Figure 1B, is not filled out by time step 30. In other words, divergence at time step 30 – again as measured by the variance – has been less than the ZFEL would have predicted in the absence of selection and constraint.

Figure 1 provides an opportunity to illustrate what we mean by a tendency. The general formulation of the ZFEL says that the *tendency* for tooth sizes to diverge is present over the entire 30 time step span. Initially the tendency is manifest, producing some divergence and an upward trend in complexity (over about the first 10 time steps). Our point is that it is still present later, even when invisible, when actual divergence is blocked (over the last 20 time steps). An implication is that if either limiting factor were removed in the thirty-first time step – say, if selection against small teeth were removed by a change in diet – divergence and the trend in complexity would resume.

Figure 1 also gives us a chance to preview of how the ZFEL can used to detect and measure imposed forces and constraints. In Figure 1A, the complexity of the set of teeth at the end of 30 time steps is the variance of the terminal histogram, and that variance is the ZFEL expectation. In other words, it is the expected complexity in the absence of selection or constraint. But if the actual divergence of the teeth follows a pattern like Figure 1B, producing less variance after 30 time steps than predicted by the ZFEL, then that difference in variance – assuming it is statistically significant – can only be the result of selection or constraint. What is more, the magnitude of the difference between the ZFEL-predicted variance and the actual variance is a measure of the intensity of selection and constraint, the intensity with which complexity has been opposed. And we can apply the same principle to detect and measure forces and constraints in cases where the actual variance is *greater* than the expected, where selection or constraint have favored diversity or complexity. We explain further in Section 4.

2.5 Constraints: Constitutive, Imposed, and Effective

The notion of “absence of constraint” in the special formulation of the ZFEL may be puzzling. A property of an object is a kind of constraint. A bear that is