# A quantitative formulation of biology's first law

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**The zero-force evolutionary law (ZFEL) states that in evolutionary systems, in the absence of forces or constraints, diversity and complexity tend to increase. The reason is that diversity and complexity are both variance measures, and variances tend to increase spontaneously as random events accumulate. Here, we use random-walk models to quantify the ZFEL expectation, producing equations that give the probabilities of diversity or complexity increasing as a function of time, and that give the expected magnitude of the increase. We produce two sets of equations, one for the case in which variation occurs in discrete steps, the other for the case in which variation is continuous. The equations provide a way to decompose actual trajectories of diversity or complexity into two components, the portion due to the ZFEL and a remainder due to selection and constraint. Application of the equations is demonstrated using real and hypothetical data.**

**KEY WORDS:  Complexity, diversity, random walk, ZFEL (zero-force evolutionary law).**

Diversity and complexity are governed by a law of evolution called the zero-force evolutionary law (ZFEL), proposed by McShea and Brandon (2010, see also McShea 2005; Brandon 2006). As originally formulated, the ZFEL was purely qualitative. Here, we offer a quantitative formulation.

We give the formal statement of the ZFEL later, but the basic principle can be stated simply here. Given two independently evolving entities, in the absence of forces or constraints acting on the differences between them, they will tend to accumulate differences and therefore to diverge, that is, to become ever more different from each other. The entities can be populations, or species lineages, or even higher taxa, in which case the divergence is an increase in diversity. Or they can be structures, "parts," within an evolving organism, in which case the divergence is an increase in the complexity of the organism. The ZFEL is a null model. It describes what happens in evolutionary lineages when forces and constraints are absent. In effect, it describes what happens when nothing happens.

The main aim of this article is to explain why ZFEL-driven divergence occurs, and to develop a quantitative method to detect and measure departures from the ZFEL expectation. Departures can arise from a variety of different configurations of forces and constraints, but any force- or constraint-driven divergence is always in addition to the baseline divergence predicted by the ZFEL. Thus, our methodological aim is to justify the idea that whenever one is investigating the evolution of diversity or complexity, the first step is to test the ZFEL null. If the ZFEL alone will produce the phenomenon to be explained, then there is no need to invoke a more complex hypothesis. Notice that we are not advocating an exclusive null hypothesis testing methodology. When the ZFEL null can be rejected, one should certainly use whatever methods are appropriate to evaluate alternative hypotheses. And of course, when the ZFEL null cannot be rejected, one is still free to investigate alternative hypotheses to explain the data. Failure to reject a null does not imply that it is true. Thus, testing the ZFEL null is a first, but by no means last, step in evolutionary investigations of diversity and complexity.

Adaptation is central in evolutionary studies. And the ZFEL has consequences for adaptation, but it is not a law about adaptation. It is only about diversity and complexity, and accordingly

it requires an adaptation-free understanding of these terms. Happily, the standard view of diversity is already adaptation free. One standard measure of the diversity of a taxonomic unit is the number of species in it, independent of how well adapted those species are, either to the physical environment or to each other. Sadly, the colloquial understanding of complexity is riddled with adaptive implications. An eye is called complex not just because it has many parts, but because they work together to perform a function and perform it well. For the ZFEL, however, we need a function-free notion of complexity, and so we adopt what has become the standard usage in the study of organismal complexity: complexity purely as number of part types, or degree of differentiation among parts, independent of how—or even whether—they function (e.g., McShea 1993, 1996). Complexity in this sense has proved useful in biology, especially for documenting evolutionary trends. Valentine et al. (1994) used number of cell types to document a trend in complexity in metazoans, and Sidor (2001) used number of skull bone types to document a (downward) trend in the complexity of tetrapod skulls. It is now also a standard usage in molecular biology, used to describe changes in numbers of genes or numbers of protein types involved in various molecular mechanisms (Doolittle 2012; Finnegan et al. 2012).

The ZFEL applies to all systems that have heritable variation. But is it important in the evolution of life on this planet (or elsewhere)? As we discuss later, there is good reason to think the ZFEL has been a major factor in the diversification of metazoan life over the Phanerozoic, but for diversification at smaller scales, we have no idea. And for complexity, the data we have on number of cell types in metazoans (Valentine et al. 1994) indicate an increasing trend, but we cannot say at this point whether that trend was driven by the ZFEL or by selection (McShea and Brandon 2010), nor do we know how the ZFEL has acted on complexity at other time and spatial scales, or for other taxa. The formulation of the ZFEL we propose here provides a way to answer these questions quantitatively. It gives a way to dissect actual trajectories of diversity and complexity into their components, the portion due to the ZFEL and the remainder due to selection and constraint, and to estimate the direction and magnitude of that remainder.

## *Diversity and Complexity*
### DISCRETE AND CONTINUOUS
In addition to diversity's discrete sense, number of types of individual or of taxa, it also has a continuous sense, degree of differentiation among individuals or taxa, or disparity (Foote 1994), often measured as a variance. Complexity too has both discrete sense, a count of part types, and a continuous sense, degree of differentiation among parts. For the continuous sense, it can like disparity be measured as a variance. As will be seen, the ZFEL applies to both diversity and complexity and in both senses.

### LEVEL RELATIVITY
Both diversity and complexity are level-relative concepts, meaning that the diversity or complexity of a system at some level has no necessary relationship to its diversity or complexity at any other level. The complexity of a fish at the level of tissues and organs is about 90, that is, it has about 90 different tissue and organ types. Its complexity at the level of cell types is about 130. And at the atomic level it is 6, if we include just the most abundant atom types: oxygen, carbon, hydrogen, nitrogen, calcium, and phosphorus. The point is that a fish has a different complexity at every level, and that these numbers could in principle be independent of each other. An animal could in principle have thousands of cell types and only a few tissue and organ types, or vice versa. Further, as there is no preferred level of analysis, a fish has no "true" complexity. Diversity too is level-relative. When the diversity of some group measured in terms of genera goes up, the diversity of species in the same group could either go up or down.

As may be clear by now, diversity and complexity are the same concept applied in different contexts. Diversity is differentiation among individuals or higher level entities, whereas complexity is differentiation within an individual.

## *The Zero-Force Law*
The ZFEL has two qualitative formulations (McShea and Brandon 2010). The first is what we call the special formulation:

> *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.*

Unleashed from forces and constraints, evolving entities—parts (for complexity) and lineages (for diversity)—change randomly, with the result that they diverge from each other, on average. Figure 1 illustrates this for a group of 10 entities, changing in a size morphospace. All of the entities start at the same arbitrarily chosen size, 20 mm. To model complexity, we could imagine a worm with 10 initially identical segments, all the same length, 20 mm. For diversity, the figure might represent an asexual population of 10 individuals of some species, all 20 mm long.

In each timestep, each entity either increases or decreases in length by 1 mm, each with 50:50 probability. The result is 10 random walks, which the figure shows over 30 timesteps. Notice that at the end of 30 timesteps, 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
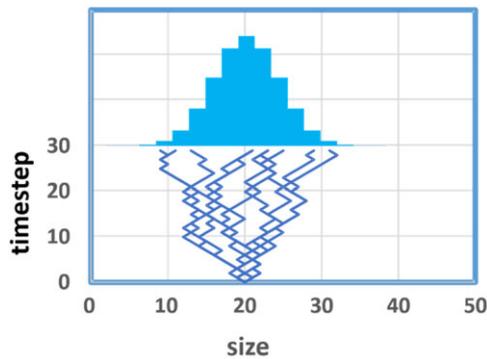
**Figure 1.** Ten entities following independent random walks over 30 timesteps. The histogram shows the distribution of outcomes for a much larger number of random walks.

tells us that the histogram approximates a normal distribution, with variance equal to the number of timesteps. Thus, 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 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 behavior is probabilistic. In any timestep, diversity and complexity may decrease, if by chance 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 "timesteps" can be thought of as generations, or million-year increments, or even longer units of time. The ZFEL principle operates on all timescales. Also, the horizontal axis is treated as an additive scale, but recognizing that change in biology tends to be proportional, one could instead interpret it as a log scale, with increases and decreases occurring in units of constant proportion.

Some may find the result—the expectation of increasing diversity or complexity—puzzling, simply because when change is random, the expected size for each lineage does not change over time. For all entities, it remains at 20. And it might seem that if the expected values for each of the two entities do not change, so that the distance between their expected values is constant, then the expected (absolute) distance between the entities themselves should not change. In fact it does. It increases. We explain later.

## THE GENERAL FORMULATION OF THE ZFEL

In the original, qualitative version of the ZFEL, McShea and Brandon (2010) also offered a more general formulation, covering the vastly more common situation in which forces and constraints are present.

*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 here is "tendency." The tendency toward increase is always present even when forces and constraints act on differences. Thus, if selection opposes the ZFEL in some evolving organism, and as a result its complexity does not increase, the tendency to increase is still present and increase begins the moment the opposing selection is removed. In other words, a tendency is a kind of push or straining toward increase. It is not an actual outcome. 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.

## RANDOMNESS

The ZFEL follows from that the fact that evolving entities change randomly when forces and constraints are absent. In population genetics, random change ordinarily means drift. And in fact, drift is the expectation for evolving lineages or parts when forces and constraints are absent. But for the ZFEL, the relevant notion of randomness is broader than drift. It includes the case in which entities change deterministically but independently of each other, that is, in which they change *randomly with respect to each other*. Thus, two snail species, one changing under selection for a wider aperture and the other under selection for a thicker shell, are changing randomly with respect to each other. Both are under deterministic selection, but independently, which means they become more different from each other but without any force acting directly on their differences. There is selection, and diversity increases—or more properly, disparity increases—but there is no selection *for* disparity. Assuming no constraints or other directed forces are acting, the zero-force condition of the special formulation of the ZFEL is met, and the resulting increase in disparity is attributable to the ZFEL. A contrast case would be two species competing for the same resource and simultaneously selected for reduced resource overlap, for avoiding competition. In that case, selection is directly *for* disparity, the zero-force condition is not met, and selection acting on their differences—not the ZFEL—is the cause of the divergence. (We will mention another contrast case later, in which two lineages diverge as they are drawn over many time steps toward different and widely separated adaptive peaks. This is not the ZFEL, because although the attracting peaks are independent, the lineage movements are not random over time, with the result that the steps are expected to be [negatively] correlated.)

## NATURAL SELECTION AND CONSTRAINTS

The ZFEL gives the null expectation, the change in diversity and complexity that would be realized in the absence of forces. The

ZFEL treats selection as a force, in that, like the various forces in physics, it has magnitude and direction. For a Newtonian analogy, think of gravity. Like gravity, selection can act with greater or lesser intensity and can act in different directions, to augment the ZFEL—driving lineages or parts further apart—or to oppose it—driving lineages or parts toward greater similarity.

The phrase "absence of constraint" in the special formulation of the ZFEL may be puzzling. We do not have space here to treat the issue in detail. For present purposes, it suffices to say that we do not intend this phrase to be understood as all-encompassing. For one thing, it covers only constraints on diversity and complexity. A constraint on, say, maximum body size, does not (by itself) limit either diversity or complexity. For another, the phrase is not intended to exclude certain constraints that we take to be constitutive of the system. For the special formulation of the ZFEL, there are two such constitutive constraints, reproduction and heredity, constraints that are fundamental to life everywhere. See McShea and Brandon (2010) for further discussion.

## UNIVERSALITY

The ZFEL for diversity applies to all populations and taxa, in all places and at all times in the history of life. The ZFEL for complexity applies to all characters, in all organisms, everywhere and always. More generally, it applies to all evolutionary systems, all systems in which there is variation and heredity. Notice that these two requirements are a subset of Darwin's three conditions for the occurrence of selection itself: variation, heredity, and nonrandom differential reproductive success. It follows that the ZFEL is at least as widely applicable as selection.

## HISTORICAL CONTEXT

The present method can be seen as an extension of studies of random walks in paleobiology pioneered by Raup (1977, see also Raup and Gould 1974) and advanced since then by Bookstein (1988), Gingerich (1993), McShea (1994), Roopnarine et al. (1999), Sheets and Mitchell (2001), Hunt (2006, 2007), and others. But even in this context, the aims are different. The concern of much of this literature has been on devising ways to detect trends and investigate mechanisms in various morphometric variables like body size. Here, we take this line of thought in a somewhat different direction, applying the methods to a second-order variable, the variance. We discuss later the relationship between the ZFEL and various phylogenetic methods.

## A Quantitative Formulation

The ZFEL gives the null expectation, the zero-force expectation. It describes what happens in the absence of selection and constraint. A quantitative formulation has two main uses. It enables us to detect the action of forces. For diversity and complexity, selection
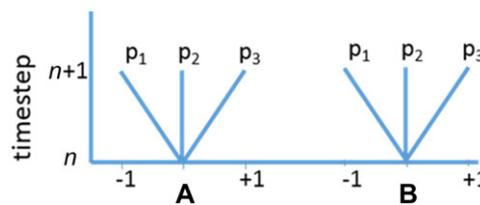


**Figure 2.** Two entities, A and B, moving in a one-dimensional space over one timestep, both with probabilities of increase, stasis, and decrease equal to 1/3, 1/3, and 1/3, respectively.

and constraint are detectable as statistically significant departures from the zero-force expectation. A quantitative formulation also enables us to measure the magnitude and direction of forces. The intensity of selection and constraint are measureable as a function of the degree of departure from the zero-force expectation.

Here, we offer two very different approaches to quantifying the zero-force expectation, one specific to the discrete case—where entities occur as discrete types—and one to the continuous case—where variation among entities is continuous. There is no suggestion here that these are the only approaches. Others are doubtless possible.

In both approaches, we develop equations to describe the behavior of the difference between—or distance between—two lineages evolving in a simple one-dimensional morphospace. We use the terms difference and distance, rather than complexity or disparity, because the equations are general and applicable equally and interchangeably to both. Finally, as we discuss briefly, the equations can be extended to more lineages, and to more dimensions, but that is beyond the scope of this article.

## QUANTIFICATION OF THE ZFEL: THE DISCRETE CASE

We start with a very simple case. Consider two entities, **A** and **B**, in a one-dimensional space with **A** to the left of **B** (Fig. 2). Each moves through time according to the following rule: move one unit to the left with probability 1/3, stay in place with probability 1/3, and move one unit to the right with probability 1/3. These three probabilities are labeled $p_1$, $p_2$, and $p_3$, respectively. For simplicity we have made $p_1 = p_2 = p_3$, but they can take any values so long as they sum to 1. There are nine possibilities for the joint behaviors of the two entities after one timestep. One of these is *stasis*. Here stasis means no part of the system changes. The result of stasis is, obviously, no change in the distance between **A** and **B**. Two other possibilities also result in no change in the initial distance between the two; when they both move to the right, and when they both move to the left. We will call this *parallel change*. Three more possibilities result in the two entities coming closer together. They are: **A** moves to the right and **B** moves to the left; **A** moves to the right and **B** stays in place; and **A** stays in place while **B** moves to the left. We call this *convergent change*. Finally, there is what we

call *divergent change*. Here the entities move further apart, which in this simple model happens when **A** moves to the left and **B** moves to the right; when **A** moves to the left and **B** stays in place; or when **A** stays in place while **B** moves to the right. Note that the four categories, stasis (*S*), parallel change (*PC*), convergent change (*CC*), and divergent change (*DC*), are qualitative.

A changes position over one timestep, if it moves to the right (with probability 1/3) or if it moves to the left (with probability 1/3). Thus, it changes with probability 2/3. We will label this probability, *r*, which denotes the rate of change per timestep. So for the system of two entities, **A** and **B**, the probability of change, or equivalently, the probability of non-stasis over one timestep, is $1 - (1 - r)^2$, because change occurs if either one or both of **A** and **B** change. (If we had a system of *k* entities the, probability of non-stasis would be $1 - (1 - r)^k$, but in this article we will restrict ourselves to comparisons of two.) We will label the number of timesteps, *t*. Stasis occurs over *n* steps only if there is no change in any of the *n* steps. Thus (where NS stands for non-stasis):

$$P\,(NS) \;=\; 1 - (1 - r)^{2n}.$$

One important consequent of this equation is that the probability of change, or equivalently the probability of non-stasis very quickly approaches 1 as *n* increases. In our example, at $n = 1$, $P(\text{non-stasis}) = 8/9$ or 0.889 to three decimal places; at $n = 3$, $P(\text{non-stasis}) = 0.9986$; and by $n = 5$, $P\,(\text{non-stasis}) = 0.99998$. Put another way, in this simple model, stasis is incredibly unlikely.

But we are not interested in the probability of change, rather we are interested in the probability of divergent change, that is, change that increases the difference between **A** and **B**. The probability of divergent change is the probability of non-stasis minus the probability of parallel change minus the probability of convergent change. We can combine parallel change and convergent change into one quantity, non-divergent change (*NDC*). Thus,

$$P\,(DC) = P\,(NS) - P(NDC).$$

Adding and subtracting *P(S)* on the right side of the above equation gives:

$$P\,(DC) = P\,(NS) + P\,(S) - [P\,(NDC) + P(S)].$$

But since change and stasis are mutually exclusive and exhaustive options in our system, $P(\text{non-stasis}) + P(\text{stasis}) = 1$. Therefore, the above simplifies to:

$$P\,(DC) = 1 - [P\,(NDC) + P\,(S)]. \tag{1}$$

We can compute the term $P(NDC) + P(S)$ directly by going through each possible move of **A** and then looking at every possible move of **B**, seeing which of those increases the difference between **A** and **B**. Figure 3 shows how this is done in practice.
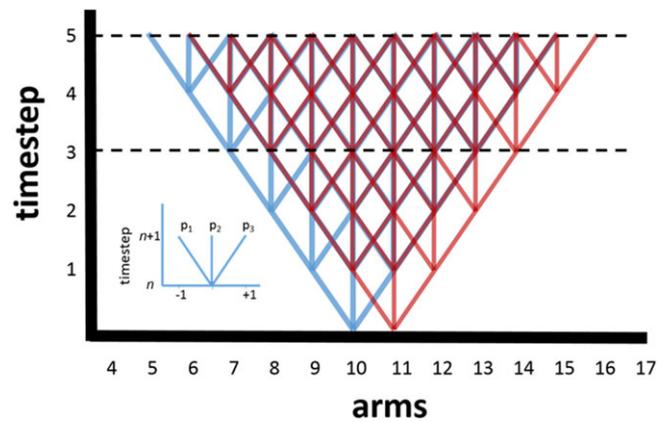


**Figure 3.** All possible trajectories for two entities, A (blue) and B (red), with starting points of 10 and 11, respectively, over five timesteps. The inset reprises Figure 2, showing the probabilities of increase, stasis, and decrease in each time step, 1/3, 1/3, and 1/3, respectively. In the discussion, the entities are two populations of sunstars, and the horizontal axis is number of arms, presumed to be strongly heritable.

The first thing to notice about the figure is that it locates **A** and **B** on a scale, in particular a scale that is metric in the sense that differences correspond to distances and also, in this section, discrete in that points on the scale correspond to whole numbers. This geometrical approach is quite versatile, in that it is applicable to many aspects of the phenotype, especially to morphology, although there are certainly some biological dimensions for which it will not work. For instance, we see no nonarbitrary way of placing the four DNA bases on such a metric scale.

Figure 3 extends our model over five timesteps. To help fix ideas here, let this figure represent two populations of sunflower starfish (also called sunstars). Sunstars vary in arm number and we assume here that arms come in whole numbers, and that arms are added or subtracted by only one over one timestep. This is a purely hypothetical example to show how equation (3) works numerically and to show why the ZFEL is a statistical necessity in the conditions described by special formulation of the ZFEL. The reader is asked to ignore developmental biology or population genetics for purposes of this example.

The one-way trifurcating lattices represent all of the possible trajectories of **A** (blue) and **B** (red). Let *A* and *B* denote the positions of lineages **A** and **B**, with $A_0$ and $B_0$ denoting their initial positions. Note that at timestep *n*, lineage **A** can take on $2n + 1$ possible values: $A_0 - n$ through $A_0 + n$.

For each possible move of lineage **A**, classify the moves of lineage **B** into two categories: divergent and non-divergent (the latter consisting of parallel, convergent, and stasis). The initial value of $B - A$ is $B_0 - A_0$; in our example we have $B_0 - A_0 = 1$. As trajectories of **B** and **A** can cross so that $A > B$, divergent

moves are ones for which either $B - A > 1$ or $A - B > 1$, that is, for which $|B - A| > 1$.

To calculate the probability of divergence, we return to equation (1) above, $P(DC) = 1 - [P(NDC) + P(S)]$. It is straightforward to calculate the sum of non-divergent change and stasis, $P(NDC) + P(S)$, in one step. We start by taking a fixed value of $A_i$ and then summing over values of $B$ that result in $|B - A| \leq B_0 - A_0$. For instance, at timestep 3, $A$ has $2n + 1 = 7$ possible states, ranging from 7 arms to 13 arms, each of which has a well-defined probability. If $A$ is in state 7, then what possible states of $B$ result in non-divergence, that is, $|B - A| \leq 1$? Figure 3 makes clear that there is only one such $B$ state, namely $B = 8$. Next, we move to state $A = 8$, where we find that there is non-divergence when $B = 8$ or 9. We continue similarly for the other possible values of $A$. Expressed as a formula, $P(NDC) + P(S)$ is:

$$\sum_{i = A_0 - n}^{A_0 + n} P(A = i) \sum_{|j - i| \leq B_0 - A_0} P(B = j).$$

This gives us a simple measure of all of the possible pairs of trajectories that leave $|B - A|$ at or below the original distance between them. It includes all of the pairs that would fit into one of our qualitative change categories (convergent or parallel), but it also includes the single case of stasis. Recall that stasis means no part of the system changes at any time. Thus, stasis excludes a trajectory that, say, moves one unit to the left, then one unit to the right. That case is one of no net change, but is still change. The trifurcating pattern of our model produces 59,049 $[= (3^5)^2]$ possible trajectories for each of $\mathbf{A}$ and $\mathbf{B}$ by timestep 5, but there is exactly one of these (one of 59,049) that is stasis, namely when $A$ stays at 10 and $B$ at 11.

Again, the double summation above is the sum of $P(NDC)$ and $P(S)$, that is, the sum of probabilities over all pairs of trajectories that leave $|B - A|$ less than or equal to 1. Now, returning once more to equation (1), $P(DC) = 1 - [P(NDC) + P(S)]$, we can calculate the probability of divergence as follows:

$$P(DC) = 1 - \sum_{i = A_0 - n}^{A_0 + n} P(A = i) \sum_{|j - i| \leq B_0 - A_0} P(B = j). \quad (2)$$

Let us see how equation (2) works over a number of timesteps. We have already gone over the result for one timestep: 1/3 of the time the system moves in parallel, 1/3 of the time it converges, and 1/3 of the time it diverges. This is straightforward given the way we have built the model. However, this result does not hold consistently. What is true of the one timestep change is not necessarily true for $n$ timesteps. We will illustrate this by considering what happens in timestep 3 and timestep 5.

Figure 3 shows the 27 possible trajectories for $\mathbf{A}$ by timestep 3. By timestep 5 there are 243 possible trajectories (blue lines). Figure 3 shows the same number of possible trajectories of $\mathbf{B}$
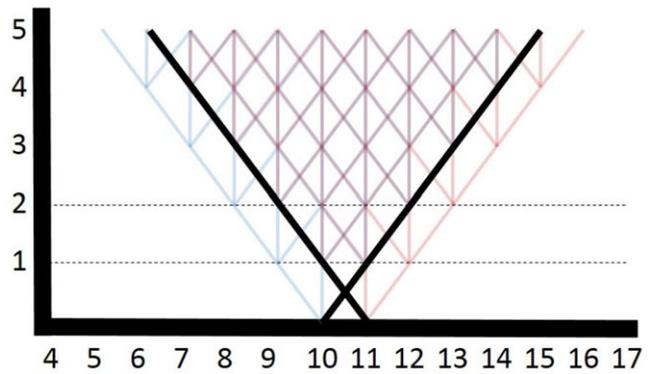
starting at position 11 rather than 10 (red lines). As we have assumed that the three basic transition probabilities are identical, it follows that every possible trajectory has the same probability. Thus, we can get the probability of a class of trajectories (say those of $\mathbf{A}$ that end up at 10) from the frequency of those trajectories. (Relaxing the assumption that the transition probabilities are all identical makes for a more complex calculation, but raises no other problems.).

As described earlier, $\mathbf{A}$ has seven possible states—ranging from seven to 13 arms—at timestep 3. If $\mathbf{A}$ is in state 7, then what possible states of $\mathbf{B}$ result in non-divergence or stasis? That is, what states of $\mathbf{B}$ result in a difference between $A$ and $B$ of less than or equal to 1? Figure 3 makes clear that there is only one such $B$ state, namely $B = 8$. Then we move to state $A = 8$, where we find that there is non-divergence in the cases where $B = 8$ and $B = 9$. Going through the remaining possible states of $A$, we can calculate $P(NDC) + P(S)$: for our example, this probability is 0.4897. This is not yet the probability of ZFEL change. To get that we subtract $P(NDC) + P(S)$ from 1, as per equation (1). So the probability of divergent change, $P(DC)$, is $1 - 0.4897 = 0.5103$.

Recall that at timestep 1, the probability of divergent change is 1/3. At timestep 2, it equals 4/9. It is not until timestep 3 that the probability of divergent change exceeds 0.50. By timestep 5, it is 0.5924. This chance of divergence continues to increase with time. How does this happen, that is, how does the unlikely at timestep 1 become likely by timestep 5? It happens because certain pairs of trajectories change their qualitative categories as they extend through time. Consider the inner envelopes of the $\mathbf{A}$ and $\mathbf{B}$ distribution of trajectories (Fig. 4). They are one unit apart at time 0 ($A = 10$, $B = 11$) and one unit apart at time 1 ($A = 11$, $B = 10$), but the ordinal relation of A and B change because the two trajectories cross each other. At time 2, $A = 12$ and $B = 9$, and so the distance between $A$ and $B$ has increased and will continue to do so.

Two things favorable to divergence are happening here. The first is the crossing of lines, which results in a qualitative change from non-divergent to divergent. That is why the result of one timestep in our example cannot be extrapolated forward. Of course, we have started our two lineages (**A** and **B**) close to each other so that the lines start crossing earlier. But there will always be only a finite distance between any two lineages and so crossing over can eventually occur.

The second thing that happens in our example is quantitative. The black lines in Figure 4 are in the divergent category by timestep 2, but they get more and more divergent with each timestep.

Thus, far we have quantified the likelihood of ZFEL change. But we can also quantify how much change is expected at any given timestep, that is, we can quantify the expected value of $|B - A|$. Here, we simply go through all possible combination of $A$ and $B$ values and calculate $|B - A|$, which we then weigh by the appropriate probability. This is shown is equation (3):

$$E|B - A| = \sum_{i = A_0 - n}^{A_0 + n} \sum_{j = B_0 - n}^{B_0 + n} |j - i| \; P(A = i) \; P(B = j). \quad (3)$$

At timestep 1, $E|B - A| = 1.222$. Recall that the probability of divergent change in timestep 1 was only 0.333, so one might wonder how this expectation could be greater than the original difference of 1. This happens because the distribution of values of $|B - A|$ is skewed. Already in timestep 1, the distance between $B$ and $A$ can be as high as 3, but $|B - A|$ can never go below 0, thus causing a right skew. By timestep 3, $E|B - A| = 1.774$, and by timestep 5, $E|B - A| = 2.199$. The expected value of $|B - A|$ continues to rise with time. This gives us a quantitative null expectation against which real world data can be compared.

## QUANTIFICATION OF THE ZFEL: THE CONTINUOUS CASE

Evolutionary change in organisms is often continuous rather than discrete. Body size varies continuously, as does everything from the dimensions of body parts to the rates of biological processes. Here we show how to calculate, as for the discrete case, the probability as a function of time that two continuously varying entities will diverge and the expected value of that divergence, that is, the magnitude of the expected increase.

Consider two entities, **A** and **B**, starting at different values along some continuous axis of variation, as shown in Figure 5. We have arbitrarily labeled that axis "size," and set the starting points at 2.0 and 3.0 mm. One can think of the entities as two species, plotted on a body-size axis, with an initial difference between them of $D$, here 1.0 mm, in which case, $D$ is their initial disparity. Or the entities could be two parts in the same individual, perhaps
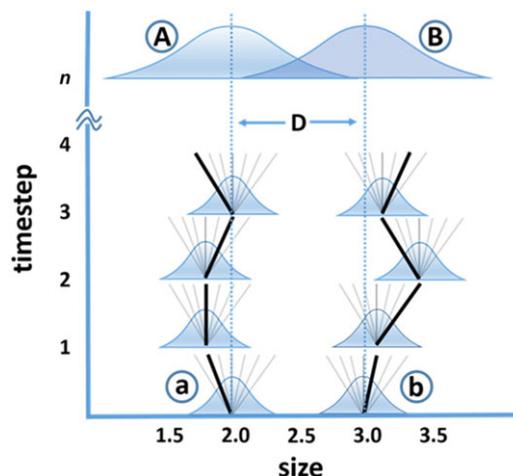


**Figure 5.** Trajectories of two lineages, A and B, initially separated by some difference, D, both following Gaussian random walks. In each timestep, each lineage changes by a value drawn from a normal step-size distribution (circled lowercase letters). The resulting distributions after *n* timesteps (circled uppercase letters) is shown above.

two teeth, in which case the initial difference $D$ is a measure of the complexity of the tooth pair.

In each timestep, each entity increases or decreases in size by some value chosen from the small normal distributions shown (lowercase a and b, with circles). These small distributions are what we call step-size distributions. To calculate the size of each entity at time 1, we draw a value from the step-size distribution and add it to the entity's value at time 0, that is, to 2.0 and 3.0 mm for $A$ and $B$, respectively. The step-size distributions have a mean of zero, so the size of each entity will increase half of the time and decrease half the time, and we have assigned them a variance, $\sigma_{ss}^2$. (We assume for present purposes that the step-size distributions for both entities are the same, although there is no reason that this assumption could not be relaxed.) Again, in this model, change is additive, but because change in biology is often proportional, the horizontal axis could alternatively be interpreted as a log scale.

The procedure is the same for later timesteps. To compute an entity's size at time 2, we draw a value from the step-size distribution and add it to the entity's value at time 1. To make the problem tractable, we assume the step-size distributions do not change with time. Continuing this procedure, each entity follows a random walk, or more precisely, a Gaussian random walk, because the step sizes are drawn from a normal distribution. Figure 5 shows a possible trajectory for each of the two entities over 4 timesteps. Extending the run to $n$ timesteps, the cumulative results are the two large normal distributions (uppercase A and B, with circles). The means of these large distribution are the same as the initial values, 2.0 and 3.0, and the difference between means is the same as the difference between initial values, $D = 1.0$ mm. The variances

of these large distributions are the sum of the variances of the step-size distributions that produced them, $n\sigma_{ss}^2$. Thus,

$$\sigma_n^2 = n\sigma_{ss}^2, \qquad (4)$$

where, $\sigma_n^2$ is the variance of the terminal distributions of each of the Gaussian random walks after $n$ steps, and $\sigma_{ss}^2$ is the variance of the step-size distribution.

We now calculate the distribution of differences between $A$ and $B$ after $n$ steps. Figure 6A shows the distribution for $B - A$. Because the distributions of $A$ and $B$ are independent, the distribution of $B - A$ is also normal, with mean equal to the mean of $B$ minus the mean of $A$ (i.e., $D$, here 1.0 mm), and variance equal to the sum of the variances of the $A$ and $B$ distributions, $2\sigma_n^2$.

Divergence occurs after $n$ steps whenever $B - A$ is greater than the initial difference, that is, whenever $B - A > D$. But there is a second route to divergence, one in which the two lineages cross so that by the $n$th step, $B$ is not only less than $A$, but less than $A$ by an amount greater than the initial difference, $D$. (This is the "crossing" discussed in the discrete case.) In these cases, the entities would have reversed their ordinal positions along the size axis, but they are still more different from each other than they started out. Thus, to capture both routes to divergence, we need to measure the increase in the *absolute* difference between the random walks, $|B - A| > D$ (or here, $|B - A| > 1.0$). Figure 6B shows the first step in calculating the distribution for $|B - A|$. The $B - A$ distribution in Figure 6A is folded over at the zero line. In effect, the negative differences for $B - A$ are converted to positive differences, in other words, to absolute differences.

We are now in a position to calculate the probability of divergence. It is the area of the folded curve in Figure 6B that is to the right of $D$ (1.0, vertical dashed line). Notice that this area is the sum of two pieces, the large right-hand half of the original $B - A$ distribution, which has an area of 0.5, plus the portion of the folded left tail of the original $B - A$ distribution that is to the right of $D$. Three features of this result are worth pointing out. First, consistent with intuition, the smaller the initial absolute difference between the entities, the larger the size of the residual folded left tail, and the closer the total probability of divergence will be to 1. When the initial difference is zero, when the entities start at the same size, divergence is essentially certain. Starting from zero disparity or zero complexity, there is nowhere to go but up. Second, the sum of the two distribution pieces will always be greater than 0.5, meaning that divergence is always the expected outcome, regardless of the initial difference. Third, notice that the reversal of ordinal position can happen in the very first timestep. The step-size distributions extend to infinity in both directions, with the consequence that—no matter how far apart the starting points and how low the variance of the step-size distribution—
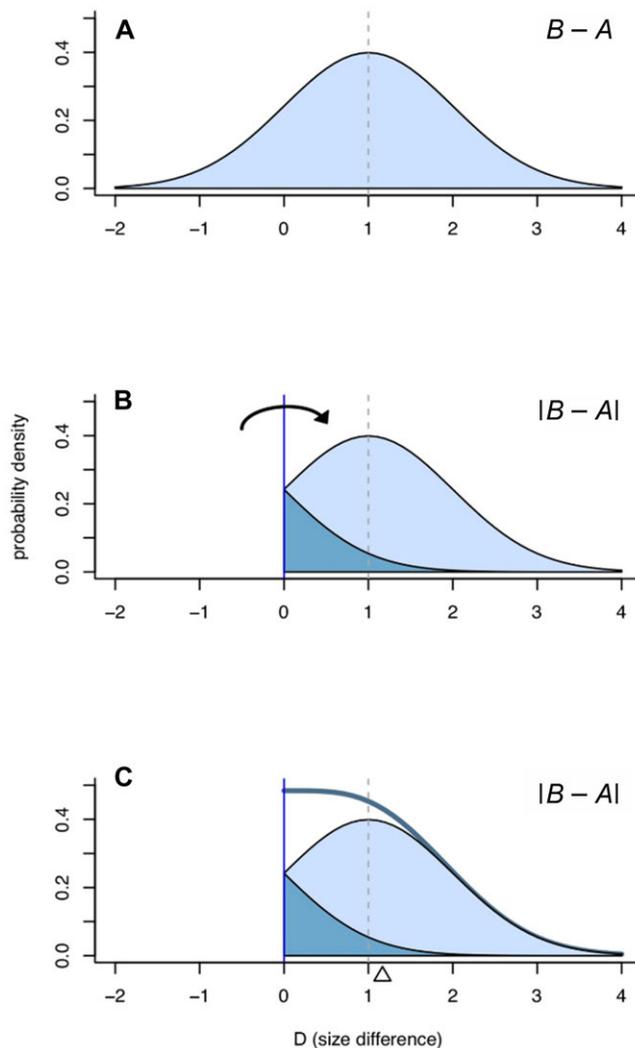


**Figure 6.** Distribution of the difference and absolute difference between two lineages, A and B, after *n* timesteps. (A) Distribution of difference between A and B, where A and B are initially separated by 1 unit. Dotted vertical line indicates initial separation. (B) The distribution of absolute differences is generated by folding the distribution in (A) about the vertical line at $x = 0$. (C) The probability density function for $|B - A|$ (heavy blue curve) is obtained by summing the curve bounding the light blue region and the curve bounding the dark blue folded region. The triangle denotes the expected value of $|B - A|$. Note that this expected difference is greater than the initial difference of 1 (shown by the dotted vertical line).

some portion of the folded left tail will extend into divergence territory, increasing the probability of divergence above 0.5.

We can now give an equation for the probability of divergence:

$$P(DC) = P(B - A) > D + P(A - B) > D$$
$$= 0.5 + \left[1 - \Phi\left(\tfrac{\sqrt{2}D}{\sigma_n}\right)\right], \qquad (5)$$

where $P(DC)$ is the probability of divergence, or the probability that the distance between the lineages after $n$ steps will be greater than $D$, the absolute initial difference between the two lineages. Also, $\sigma_n$ is the standard deviation of the terminal distribution of either of the random walks, and $\Phi$ is the standard normal cumulative distribution function. Notice that this equation is the analogue of equation (2), which gives the probability of divergence in the discrete case.

Finally, we can calculate the expected value of the $|B - A|$ distribution, in other words, the expected absolute difference between A and B after $n$ steps. The $|B - A|$ distribution belongs to a class of well-known folded-normal distributions. Figure 6C shows the distribution after folding; the expected value can be calculated as:

$$E\,|B - A| = \frac{2}{\sqrt{\pi}}\sigma_n \times \exp\left(\frac{-D^2}{4\sigma_n^2}\right) + D\left[1 - 2\Phi\left(-\frac{D}{\sqrt{2}\sigma_n}\right)\right], \quad (6)$$

where $E|B - A|$ is the expected absolute difference between $A$ and $B$, $\sigma_n$ is the standard deviation of the terminal distribution of either of the random walks ($= \sqrt{n}\,\sigma_{ss}$), $D$ is the absolute initial difference between the two lineages, and $\Phi$ is the standard normal cumulative distribution function. Consistent with the prediction of the ZFEL, $E|B - A|$ increases monotonically with time, or in other words, the expectation is always an increase in disparity or complexity. Notice that this equation is the analogue of equation (3), which gives expected values in the discrete case. (Eqs. 7 and 8 in Supporting Information Appendix 1 express $P(DC)$ and $E|B - A|$ in terms of $\sigma_{ss}$, which makes for a more direct computation in some circumstances.)

We can now use these results to demonstrate how the ZFEL can be applied to certain kinds of data. Hunt et al. (2010) studied a body-size trend in deep-ocean ostracods over the past 40 million years. They found a general trend toward increased size and argued that it was driven by deep-ocean cooling over much of that period. However, they also identified a 16 million year period during which the cooling paused, the trend disappeared, and the pattern of change in ostracod lineages was consistent with a random-walk model. Figure 7 shows the pattern during that interval.

For our purposes, we are interested in disparity, the difference in body size between pairs of lineages and their divergence over time. Table 1 shows probabilities of divergence as well as actual absolute differences and the absolute differences predicted by the ZFEL, all for a select sample of lineage pairs from Figure 7. Supporting Information Appendix 1 explains how the calculations were done, and Supporting Information Appendix 2 gives the R code.

The left side of Table 1 shows results over a five million year span for four lineage pairs that start close together (column 1). In particular, it shows the starting difference (column 2) and the
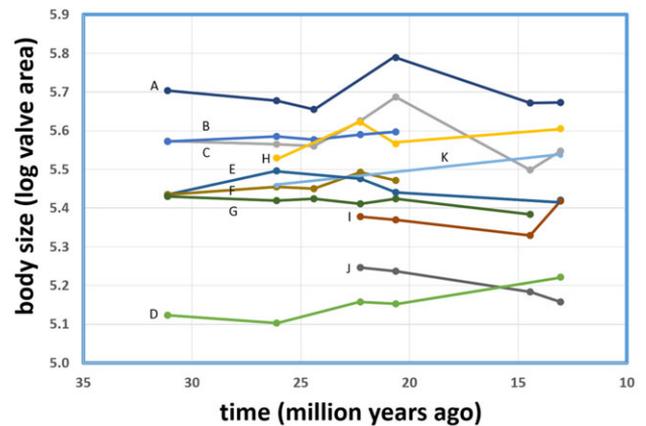


**Figure 7.** Body-size trajectories for deep-ocean ostracods. Data are from Hunt et al. (2010). See text for discussion. See Supporting Information Appendix for species identification and numerical data.

probability of divergence over five million years (column 3). This is the probability that disparity would increase over the starting distance, on the assumption that change in disparity was driven by the ZFEL alone. Column 4 shows whether the lineages actually converged (conv) or diverged (div). The left side of the table also shows the disparity predicted after five million years by the ZFEL acting alone (column 5), the actual disparity after 5 million years (column 6), and a $P$-value for the difference between the two (column 7).

The lineage pairs in the left half of the table were chosen because the starting sizes of the two lineages were nearly the same, in other words, the starting disparity was near zero. In such a circumstance, disparity is extraordinarily likely to increase and unsurprisingly it did so in all four pairs (column 4). The ZFEL must have been partly responsible for this increase, but the magnitude of the increases is potentially revealing. In principle, one or more these divergences could have been encouraged by competitive displacement, that is, selection favoring nonoverlap among body sizes. In that case, the spread of terminal sizes would be the result of selection for diversity, as well as the ZFEL, and the spread should be greater than predicted by the ZFEL alone. However, for these four lineage pairs, none of the actual divergences (column 6) is significantly greater than the divergence expected due to the ZFEL alone (column 5). In other words, none of the $P$ values in column 7 attain statistical significance ($P < 0.05$), consistent with (although of course not conclusively demonstrative of) the interpretation that selection for diversification did not play a significant role.

Another feature of the left side of Table 1 is worth a remark. As the initial absolute difference increases (*EF* to *BC* to *EG* to *FG*), the probability of increase—that is, the probability of ZFEL-driven divergence—decreases (column 3). The reason is

**Table 1.** Actual and expected absolute differences between selected lineage pairs.

| Lineage pair (1) | Absolute difference (2) | P(div) (3) | Div/conv (4) | Expected absolute difference (5) | Actual absolute difference (6) | P (7) | Lineage pair (8) | 26.12 (mya) (9) | 24.39 (10) | 22.27 (11) | 20.63 (12) | 13.06 (13) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Initial close spacing | 31.12 mya = start | At 26.12 mya | At 26.12 mya | At 26.12 mya | At 26.12 mya | | Initial moderate spacing | Starting absolute difference | Actual abs diff (d/c) (expected) | Actual abs diff (d/c) (expected) | Actual abs diff (d/c) (expected) | Actual abs diff (d/c) (expected) |
| EF | 0.001 | 0.982 | div | 0.03600 | 0.042 | 0.35 | BC | 0.020 | 0.016 (c) (0.027) | 0.036 (d) (0.036) | 0.090 (d) (0.041) | |
| BC | 0.002 | 0.965 | div | 0.03603 | 0.020 | 0.66 | EH | 0.033 | | 0.146 (d) (0.042) | 0.126 (d) (0.047) | 0.185 (d) (0.064) |
| EG | 0.004 | 0.930 | div | 0.03613 | 0.078 | 0.08 | CH | 0.035 | | 0.004 (c) (0.043) | 0.120 (d) (0.048) | 0.059 (d) (0.065) |
| FG | 0.005 | 0.912 | div | 0.03621 | 0.036 | 0.43 | FG | 0.036 | | 0.082 (d) (0.044) | 0.046 (d) (0.048) | |
| | | | | | | | EF | 0.042 | | 0.017 (c) (0.048) | 0.030 (c) (0.052) | |

that for any fixed time interval, as the starting distance between lineages increases, the probability that they will cross decreases, and as discussed earlier, it is the crossing that produces the expected ZFEL divergence. In the extreme case, where the initial separation is very large, the probability of crossing would drop to near zero, and the ZFEL expectation would be that the terminal difference will be nearly the same as the initial difference, $D$. Still, as pointed out earlier, the probability of divergence will always be greater than 0.5, and the expected divergence always greater than $D$.

The right half of Table 1 shows actual and expected changes in diversity as a function of time for six lineage pairs. The starting point for all pairs was 26.12 mya, at which time the members of each pair were a moderate distance apart. For all pairs, the dataset is complete enough to show changes in their disparity at a number of times over a relatively long span. Consistent with expectation, in a pure-ZFEL system, the frequency of divergence increased with time: at 22.27 mya, there were three divergences and two convergences; at 20.63 mya, there were four divergences and one convergence; and at 13.06 mya, both pairs for which data were available were divergences. Also, consistent with a central claim of the ZFEL in the continuous case, divergence is the expectation for all pairs at all timespans. That is, all expected values (parentheses) are greater than the starting distances. Of course, in a pure-ZFEL world, change is probabilistic, so divergence is just the expectation. As the table shows, convergence is still possible and does occur.

The purpose of this exercise is to demonstrate the application of the ZFEL null to a real dataset, but we will say a word about interpretation of this result. First, several caveats: the pairwise comparisons may not be independent of each other, so these results alone may not tell us very much about processes acting at the level of the clade as a whole. Also, the ZFEL is a null hypothesis, and the fact that the data are consistent with it does not

imply the null is true. These considerations aside, if the null *is* true, then it implies that selection has not acted to drive lineages apart by some mechanism like competitive displacement. Finally, it is worth reiterating that the ZFEL itself is consistent with more than one hypothesis of change, such as drift or independent adaptive peaks (see below), which in turn suggests possible further investigations.

# Alternative Evolutionary Mechanisms

The range of causal mechanisms underlying change in diversity and complexity is enormous. Here, we review some of the more commonly invoked ones and describe their relationship to the ZFEL. As we have seen, the ZFEL corresponds to all situations in which two lineages (or parts) experience no consistently applied forces, and the resulting trajectories are therefore expected to be uncorrelated. The focus in this article is on divergence, and on detecting force-driven divergence that is significantly greater than the ZFEL expectation. But of course the ZFEL null can also be rejected for convergence, when the distance between two entities is significantly less than the expectation, what might be called a "lower tail" rejection. For purposes of this theoretical discussion, we consider both.

## DIVERSITY

1. Drift. Two lineages undergoing random genetic drift will tend to diverge. As discussed, this is the ZFEL.
2. Displacement. Two species competing for the same resources will tend to displace each other, and to diverge. The process goes by a number of names, including competitive displacement. It is also one aspect of Darwin's principle of divergence (Fleming 2013). Competitive displacement is selection for difference, in other words, change where the driving force is the

selective advantage, not of some particular adaptation but of being different. It is not the ZFEL, and can lead to rejection of the ZFEL null. The same occurs when one lineage is selected for similarity to the other, as occurs in the various forms of mimicry, which can lead to lower tail rejection.

3. Attraction to independent adaptive peaks. If two lineages are acted upon by different selective forces, and if those forces are independent of each other, then they are expected to change randomly with respect to each other. And that is the ZFEL. The two snail species discussed earlier are an example. However, it is not the ZFEL when peaks move systematically in a way that drives divergence, as might occur in a coevolutionary arms race. The same is true when peaks are stable but widely separated so that the two lineages are consistently drawn further and further apart over many timesteps, so that the forces experienced by the two lineages are not random from one timestep to the next. Both cases can lead to rejection of the ZFEL null.

Finally, it is also not the ZFEL when two peaks that are very close to each other draw the two lineages together over a number of timesteps, producing convergence and the potential for lower tail rejection of the ZFEL. Stabilizing selection acting on both lineages can also lead to lower tail rejection.

## COMPLEXITY

1. Drift. Two parts in a species that are not under selection or constraint will drift and therefore tend to diverge. As for two lineages, this is the ZFEL.
2. Selection for difference. The asymmetrically positioned ear openings in some owls may have been the result of selection for better sound localization. If so, then it was selection for differentiation of ear location, not independent selection on each ear. That is, it was selection for complexity and not the ZFEL. Likewise, selection for subfunctionalization, the splitting of a task among parts—such as perhaps the differentiation of mouth parts in arthropods—is not the ZFEL. In general, selection arising from the advantages of the division of labor among parts is selection for complexity and not the ZFEL. Of course, selection can also favor convergence of part types, when a functional advantage arises from similarity. For example, in the evolution of the vertebral column in whales, the vertebrae became simpler and more similar to each other, compared to those in the highly differentiated columns of terrestrial whale ancestors. This may have been the result of selection for vertebral similarity, for a column that could function as a simple flexible rod in locomotion. If so, this was not the ZFEL, and the trajectories for any two vertebrae could produce a lower tail rejection of the ZFEL null.
3. Attraction to independent adaptive peaks. The argument here parallels the one above for diversity. When two parts are acted upon by selective forces that are independent of each other,

they are expected to change randomly with respect to each other. And that is the ZFEL. For example, one tooth in a tooth row might be briefly selected for one function while another is selected for another unrelated function. Likewise, the standard explanation for duplication and selective divergence of genes is also the ZFEL. However, it is not the ZFEL when peaks are widely separated so that the two parts are consistently drawn further and further apart over many timesteps, that is, so that the forces acting on the parts are not random over time. Instead, there are consistently acting divergent forces, which in turn can lead to rejection of the ZFEL null. This last mechanism was implicit in the notion of duplication and differentiation of parts advanced by early twentieth century paleontologists (Williston 1914, Gregory 1935). In early terrestrial vertebrates, anterior vertebrae were selected for a new function, head support, in addition to the older function of transmitting swimming forces. As a result, anterior and posterior vertebrae became more different, increasing column complexity. To the extent that this was the result of adaptive forces acting consistently over a many timesteps to pull the parts toward different morphologies, along trajectories that were negatively correlated with each other, the result was not the ZFEL, and the expectation is that ZFEL null would be rejected.

4. Complexity ratchets. Decades ago, Saunders and Ho (1976) proposed that complexity would tend to increase in evolution because existing parts tend to become integrated into development and therefore difficult to remove, whereas new parts could be added without disrupting present function. Recently, the idea has been developed more fully under the heading of "constructive neutral evolution," or CNE (Stoltzfus 1999; Lukeš et al. 2011; Brunet and Doolittle 2018). In CNE, dependencies arise between initially useless parts and functional ones such that the useless ones become locked in, and their removal is selected against. CNE is ZFEL-like in that it invokes the random addition of new part types, but differs in that it requires selection to block reversals. Another ratchet, proposed by (Lynch and Conery 2000; Lynch and Force 2000), occurs when neutral additions in DNA go to fixation in small populations. Despite their affinities to the ZFEL, neither of these is a pure ZFEL process. The ZFEL has no requirement for negative selection or small population size. The ZFEL also does not require that new parts have a neutral origin. New part types can arise when existing parts are selected for new functions (as in the tooth example above), that is, when they change randomly with respect to other parts.

Still other ratchets are possible. For example, it could be that 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). Again, none of these complexity ratchets involves a purely ZFEL process, and all are expected, when they operate, to lead to an increase in complexity above that predicted by the ZFEL.

5. Constraints on complexity. When variation is constrained by development, parts may fail to diverge, leading to lower tail rejection of the null. Examples include the constraints imposed by the body plan in multicellular organisms. Insects have three body regions, vertebrates have a notochord at an early life stage, and so on. Variants in body plan features either do not arise because development is canalized, or they arise but the organism is inviable (internal selection). In either case, the result is that the differentiation of part types is limited, possibly leading to a lower tail rejection of the ZFEL. In other words, divergence fails because the absence-of-constraint-requirement of the ZFEL is violated.

The phenomenon of DNA saturation deserves some mention. When a gene with two copies evolves neutrally, both copies eventually become fully randomized and stop diverging. When this happens, divergence can be seen as limited by the number of nucleotides, four. In present terms, this is a constraint imposed by the chemistry of DNA. If a fifth nucleotide was introduced, complexity could again increase. Again, this sort of constraint can underlie a lower tail rejection of the ZFEL null.

## The ZFEL and Phylogeny

"Nothing in comparative biology makes sense except in the light of phylogenetics." Surely someone has said that, but if not, we are willing to assert it here. One then might wonder about why phylogenetics has played no role in what we have done so far. The answer to that should be clear. We are attempting to show what happens in the bare minimal model of evolution, that is, in systems with only heritable variation. We have shown that such systems diverge from one another with a quantifiable regularity. Selection, constraints and phylogenetic relationships are, in our view, to be layered in later.

Many important questions in evolution are explicitly phylogenetic. For instance, does evolution typically proceed in rapid bursts of disparity within a higher taxon followed by long periods of speciation with much less phenotypic change (Gould 1989)? Or is evolution after branching a more conservative process where ecological niches are preserved longer than would be expected under a purely random process (what is called niche conservatism, see, e.g. Ackerly 2009)? And what is the relationship between divergence and species interactions (e.g., Nuismer and Harmon 2015; Drury et al. 2018)? None of these questions can be addressed empirically without putting the taxa into a phylogeny.

A large literature of phylogenetic comparative methods has developed to address these questions. Most basic are Brownian motion (BM) models (Felsenstein 1973, 1985). Ornstein-Uhlenbeck (OU) models (Lande 1976; Hansen 1997) add to the BM model a parameter that represents the strength of return to some optimal trait value. Further variations are possible. We have to leave to the future any attempt to give anything like a precise account of the relationship of our work to this large body of literature. But there are a few basic points we can make here. Although our approach shares much with the BM approach, unlike that approach we have shown that the rate of diversification will decrease with increasing distance between lineages. The logic behind this has, we think, been well explained by our mathematical models. The closer two lineages are, the more frequent are "crossing-over" events (that is when convergent trajectories cross and become divergent), and thus the faster is the rate of divergence. Put into a phylogenetic context, this does predict a more rapid rate of diversification just after a splitting event, but with a gradual slowdown of that rate. Thus, the ZFEL, when operating alone, produces a pattern that fits neither a rapid burst model, nor a pure BM model. This, we have argued, is the appropriate null expectation.

## Discussion: The Uses of Quantification

The quantitative version of the ZFEL developed here makes it possible to answer a number of long-standing questions in evolutionary biology.

### COMPLEXITY

Aside from the Valentine et al. (1994) study of cell type types in metazoans and a few smaller scale studies (some cited earlier), very little is known about the trajectory of complexity over the history of life. To appreciate the size of the data gap, recall that complexity is, like diversity, a level-relative concept, which means that the trajectory could well be different at every hierarchical level. An upward trend in cell types does not mean that there was an upward trend in complexity at the level of organs, tissues, or molecules. Thus, it is in some ways premature to talk about the ZFEL and the causes of change. It would be helpful to first understand the pattern to know what we need to explain.

Still, there has been a modest amount of theorizing, especially recently, in treatments of CNE and other ratchets, discussed earlier. CNE is ZFEL-like, as discussed, but it is not the ZFEL, and the methods developed here could be used to detect it. In any case, perhaps this small surge of interest in CNE can motivate the development of datasets suitable for investigating how frequently the proposed ratchets have operated. The same goes for other proposed drivers of complexity. For example, complexity has been

said to be advantageous on account of the advantages of the division of labor (discussed in McShea 1991, 1996). The suggestion has been made that selection generally favors greater body size, which in turn produces selection for complexity, because larger organisms require greater division of labor (Bonner 1988). The argument has, perhaps, seemed too obvious and sensible not to be true, but even if true, we do not know how pervasive this mechanism has been in the history of life. The ZFEL provides a way to investigate that.

## DIVERSITY

The standard explanation in paleoecology for the diversification of plant and animal life over the Phanerozoic, the past 540 million years, is lineages changing under independent selective forces. This is implicitly the ZFEL. One starfish species is under predation pressure favoring a spinier skin, whereas another faces pressure to survive longer periods of desiccation. Continental drift breaks a land mass into two, so that two closely related snail species become separated and diverge as they track independently changing environments. Lineages are not changing randomly as they would under drift, but they are changing randomly with respect to each other, independently. Thus, if the standard view is correct, the diversification of multicellular life is the ZFEL in action.

One major alternative is selection for divergence. Two species competing for the same resources will tend to displace each other, and to diverge. This is not the ZFEL. Competitive displacement is doubtless quite common, say, in the divergence of sister taxa. But arguably it must be rare in evolution generally, because most species pairs do not overlap or compete much in their resources use. A beetle species does not overlap much with a species of cyanobacteria. Bats do not overlap much with whales. And thus, for most pairwise combinations of species, displacement cannot have been a significant driver of their divergence over most their history. Consider the following simple calculation. Assume that there are about eight million eukaryotic species (Mora et al. 2011). It follows that there are 31,999,996,000,000 possible species pairs in this group of eight million. There are two requirements for the competitive displacement hypothesis. One is spatial and temporal overlap, and the second is ecological similarity for which phylogenetic closeness is a good proxy. Thus let us suppose competitive displacement occurs only between two recently split sister species so that each species competes with exactly one other in a way that leads to competitive displacement. On this assumption, there are four million competitive pairs of eukaryotic species. Thus, the fraction of the total number of species pairs that could possibly fall under the competitive displacement hypothesis is about four million over 32 trillion. That is 0.000000125. Notice that our estimate of four million competitive pairs could be off by several orders of magnitude and yet the percent would still stay very,

very small. This is not to say that competitive displacement is not important in evolution (see Pfennig and Pfennig 2012), but it does not go very far in explaining the macro-pattern of biological diversity.

Another major alternative to the ZFEL involves fixed and separate adaptive peaks. Whales and bats do not compete, but suppose that in the divergence of those two lineages, the whale lineage has steadily been attracted to the preexisting whale adaptive peak, whereas the bat lineage has steadily been attracted to the bat adaptive peak. If those peaks are distant from each other, then the increasing difference between those two lineages is explained. This is an alternative to the ZFEL because it does not involve different lineages evolving randomly with respect to each other. But it faces serious difficulties. First, it invokes the idea of preexisting niches, which ignores the ecological reality of complex evolutionary dynamics involving coevolution and niche construction (Odling-Smee et al. 1996; Brandon and Antonovics 1996). Second, even if there are strong attractors in morphospace, such as wings or camera eyes, it does not follow that every aspect of morphology and behavior will be dragged along in a predetermined way. Thus, those other aspects of phenotype would be subject to ZFEL differentiation. The hypothesis that macrodiversity is explained by the existence of distant fixed adaptive peaks is limited at best.

Besides these two, we see no other major alternative to the ZFEL. But if there is not another major alternative, and if these two can at best explain a small fraction of cases of diversification, then we are in a position where the failure to reject the ZFEL null is particularly informative. If data falls well within the ZFEL expectations, as the ostracod data analyzed above does, then we have good reason to accept the ZFEL as the main driver of diversification in these cases. In any case, the tools developed here enable us to investigate this directly. Applying them across a large number of cases would allow us ultimately to draw broader conclusions about the role of the ZFEL versus alternative mechanisms in explaining life's diversity.

## CONFLICT OF INTEREST
The authors have no conflicts of interest.

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table A1.** Based on data from Hunt et al. (2010).
**Appendix S1**
**Appendix S2**