Variance, Selection and Evolutionary Explanation

by

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V. Louise Roth

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor in Philosophy in the Department of
Philosophy in the Graduate School
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ABSTRACT

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Abstract

This dissertation presents some of the first work written and published on the Zero Force Evolutionary Law (McShea and Brandon 2010). It is a collection of four philosophy of biology papers about evolutionary explanation, which together, illustrate the importance of the Zero Force Evolutionary Law (ZFEL) spanning evolutionary studies. In particular, this dissertation includes issues in the history of philosophy of science (chapter 1), group formation and network theory (chapter 2), biological hierarchy and the major transitions in evolution (chapter 3), and the Price equation and quantifying evolutionary change (chapter 4). While these four chapters may differ in focus, they make the same general claim: evolutionary methods and explanations are improved when the underlying tendency of biological systems is characterized correctly as exhibiting increasing variance.

The first chapter is a somewhat longer version of the paper, “The Notion of Limited Perfect Adaptedness in Darwin’s Principle of Divergence”, which was accepted on August, 22nd, 2011 for publication in Perspectives on Science. This chapter introduces the ZFEL historically, and it is not until the end of the chapter that the relevance of the ZFEL to Darwin’s theories is made clear. Generally, this chapter is about Darwin’s expectation of stasis in the absence of selection, which was the result of his prior belief in
limited perfect adaptedness. It was this incorrect assumption that caused Darwin difficulty when presenting his principle of divergence.

The second chapter, “Network Theory and the Formation of Groups without Evolutionary Forces” was accepted on October 4th, 2011 and published online October 20th, 2011 and in print in 2012 in *Evolutionary Biology* volume 39, pp. 94-105. This chapter presents a random network model modified to include the assumption of increasing variation, i.e. the ZFEL zero-force expectation. This results not only in the formation of groups, but also in a higher probability of group formation than is found in a model that is purely random, which illustrates how groups can form spontaneously in the absence of evolutionary forces.

The third chapter, “The Origin of New Levels of Hierarchy and Why Selection is Not the Answer” is inspired by and based on the technical results from chapter two. It explains how the emergence of biological hierarchy is largely a story of randomness, not selection. The focus is on distinguishing the question of level maintenance from the question of level origin. Though the former depends on selective factors, the latter does not. A version of this chapter is currently being reworked with Robert Brandon for publication.

Finally, the fourth chapter, “Quantifying the Zero Force Evolutionary Law” presents the first mathematical representation of the ZFEL using the framework developed by Price (1970), and demonstrates that the ZFEL is inherently true in this
framework. Using this formulation, this chapter investigates 1) the ZFEL as a background tendency in evolutionary systems, 2) the ZFEL as a strongly driven trend over the history of life, 3) the ZFEL as an emergent phenomenon at every level of hierarchy, and 4) the applicability of the ZFEL outside of biology. A version of this chapter is currently being reworked with Tim Schwuchow for publication.

Although this dissertation is composed of four distinct papers, I believe it tells a story about evolutionary explanation in biology’s past (chapter 1), present (chapters 2 and 3) and future (chapter 4). At each step it becomes clearer that evolutionary explanations are more accurate and complete when they recognize that evolution is the result of selective forces operating against a background condition of increasing variance over time.
Dedication

This dissertation is dedicated to my father, a philosopher who has always supported me despite wondering if what I do is actually philosophy, and to my mother, a non-philosopher who has always supported me despite wondering what it is that philosophers actually do.
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Thanks also to four anonymous referees (two for chapter 1, two for chapter 2) for helpful suggestions and comments. I am incredibly thankful to Tim Schwuchow for helping me create the equations in chapters 2 and 4, as well as spending many hours discussing chapter 4 with me and working with me to clarify it. And finally, thanks to Tim Schwuchow, Paige Conn, and my parents, for always being there to listen to me complain and combatting my pessimism with enthusiasm, optimism, and love.
1. Darwin’s *Origin* Diagram: Adaptation, Environment, and the Principle of Divergence

Darwin begins *On the Origin of Species* by asking the reader to “reflect on the vast diversity of the plants and animals which have been cultivated” (1859, p. 7); almost five-hundred pages later, he closes by having the reader consider the “endless forms most beautiful and wonderful” that have evolved (1859, p. 490).

Darwin contemplates diversity throughout the *Origin* and presents the principle of divergence as a way to explain it. Darwin formulated the principle of divergence around 1857 (Browne 1980), at which point he began replacing his previous view of “limited perfect adaptedness” with a view of relative adaptedness (Ospovat 1981; Burian 1983). Proponents of perfect adaptedness, such as Paley and Cuvier, argued that in God’s harmonious system, organisms are perfectly adapted to their environments, and thus, do not change. Darwin, along with many of the leading biologists of the time, revised the idea to include limitations on perfection based on the laws of matter (Ospovat 1981, pp. 34-8). This revised view is now referred to as “limited perfect adaptedness.” A major difference with this limited view is that it allows environmental variation to disrupt the harmony between organisms and their environment, causing them to change and evolve as a reaction to unstable conditions. Organismic variation only occurs when environmental conditions are altered, and the purpose of such variation is to direct organisms back toward perfect harmony.
Ospovat argues that Darwin held a view of limited perfect adaptedness when writing the “Essay of 1844” and the “Sketch of 1842” (Darwin and Darwin 1909), but that by the publication of the *Origin*, a notion of relative adaptedness had completely replaced the former teleological view. According to Ospovat, “with the full development of the principle of divergence, relative adaptation became a necessary implication of his theory” (1981, p. 206). While I agree that in 1844 Darwin certainly held a concept of limited perfect adaptedness and that relative adaptedness is a necessary implication of the principle of divergence, I disagree with Ospovat’s claim that Darwin completely gave up his notion of limited perfect adaptedness when formulating the principle of divergence. Relative adaptedness requires a varying environment and competition, and although most of what Darwin writes about divergence hinges on these two ideas, his diagram includes species that leave slightly altered or unaltered descendants after thousands of generations. These non-diverging species must be in an environment where there is little or no variation or competition, and their unchanging nature, I argue, is explained by a notion of limited perfect adaptedness.

In the following section I introduce Darwin’s notion of relative adaptedness to motivate the distinction between relative and perfect adaptedness. Next, I present Darwin’s *Origin* and *Natural Selection* diagrams, and then discuss the three different types of environments illustrated in these diagrams. The first two environments require
a notion of relative adaptedness and the third requires a notion of limited perfect adaptedness. I then discuss in more detail why the notion of limited perfect adaptedness is necessary. Finally, I conclude the chapter with a reinterpretation of the pattern in Darwin’s *Origin* diagram, inspired by the Zero Force Evolutionary Law, including a discussion of how the pattern is understood today.

1.1 *Darwin’s Two Types of Relative Adaptation*

Ospovat argues that Darwin had two types of adaptation in mind (1981, p. 206) when he replaced the idea of limited perfect adaptedness with relative adaptedness. There is the sense that (1) “the adaptedness of every species is relative to the adaptedness of other species” (1981, p. 206) and that (2) “all of the competing species that at a given moment are approximately equally well adapted may become still better adapted in comparison with, say, the species of another country” (1981, p. 206). Burian labels the first “Relative engineering fitness” and the second “Selected engineering fitness” (1983, p. 293). In the first type, the emphasis is on the adaptedness of an organism in relation to all the other organisms it is competing with in a specific environment, or a “real environmental challenge,” as Burian calls it. With the second type, the focus is instead on organisms that are already well adapted or “fit” because of their evolutionary history; however, because environments change, “There is always room for improvement” (Ospovat 1981, p. 206). What is important about these two types of adaptation (or relative engineering fitness versus selected engineering fitness) is
that they both require unceasing variation in nature. It is also useful to note that under a view of limited perfect adaptedness, natural selection is limited by the type of variation that arises, the purpose of which is to realign organisms with their altered environment. As Burian says, “Once Darwin came to realize that variation is ubiquitous and largely undirected with respect to the needs of the organism, he was forced to employ a relative concept of adaptedness, a concept tied much more intimately to the process of natural selection than the absolute one was” (1983, p. 291, my emphasis). Similarly, Ospovat says that

When he wrote the “Essay of 1844” Darwin assumed that variation occurs only as a result of environmental change; in *Natural Selection* he assumed that it is always occurring because conditions never remain absolutely unchanged. In 1844 an increase in food is allowed to be perhaps a minor cause of variation; in *Natural Selection* it is said to be an important cause; and by 1868 Darwin called it probably the single most powerful cause. (1981, p. 208, my emphasis)

The main argument of this chapter is the following: According to Darwin, when there is variation, there are diverse descendants, and when there are diverse descendants, there is selection for divergence; however, in Darwin’s diagram, divergence does not occur everywhere, meaning variation must not occur everywhere either. I am not arguing that Darwin held the same concept of limited perfect adaptedness as he did in 1844, but that it was still influential in his thinking. In Darwin’s diagram there is an environment where species do not diverge, descendants do not vary, and conditions remains absolutely unchanged, and this is only understood by employing a notion of limited perfect adaptedness.
1.2 Darwin’s Origin Diagram

Darwin discusses the principle of divergence during the second half of chapter four in *On the Origin of Species*. To illustrate his principle, he presents the only diagram found in the *Origin* (see Figure 1). Letters A through L represent species\(^1\), the lowercase letters a\(^1\) to z\(^1\) represent varieties (incipient species), and numbers I through XIV represent time intervals, each 1000 generations long (Darwin 1859, p. 117).\(^2\) The x-axis represents character-space, so letters ‘A’ and ‘I’, for example, represent species that are very disparate with respect to their morphological, or rather, character, traits. Species (A) through (L) also vary in size, specifically, Darwin states that species (A) and (I) are wide-ranging and common.

From a cursory glance, one can see that after Darwin’s hypothetical 14,000 generations, only species (A), (F) and (I) have left descendants. Darwin says “The intermediate species, also (and this is a very important consideration), which connected the original species (A) and (I), have all become, excepting (F), extinct, and have left no descendants” (1859, p. 123).

\(^1\) Darwin also says at one point that letters A through L need not be species and asks the reader to imagine they are genera: “We may suppose that the numbered letters represent genera, and the dotted lines diverging from them the species in each genus...The horizontal lines may represent successive geological formations, and the forms beneath the uppermost line may be considered as extinct” (1859, p. 331).

\(^2\) Darwin says “The intervals between the horizontal lines in the diagram, may represent each a thousand generations; but it would have been better if each had represented ten thousand generations” (1859, p. 117, my emphasis). Most likely he stressed this because of his belief in gradualism.
Figure 1: Darwin’s only diagram in *On the Origin of Species* illustrating the "Divergence of Taxa" that occurs, in this case, over 14,000 generations (each horizontal line represents 1000 generations). Letters A through L represent species while the lowercase letters a to z are more likely termed varieties (incipient species). The x-axis represents character-space, that is, differences in character traits.

The number of species (or varieties) only increased from 11 to 15, however, those 15 species have diverged and are much more disparate than the original 11. Although

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3 Darwin’s notion of varieties is a loose and continuous concept containing groups that just recently diverged from their parent species and groups that have persisted but are not yet species: “…varieties are species in the process of formation” (1859, p. 111). By the time Darwin wrote the *Origin* he no longer had a rigid species concept and was content with the idea of continuity between groups, varieties, and species, for this agreed with his principle of divergence. He says in chapter two that “the term variety, again [like with the term species], in comparison with mere individual differences, is also applied arbitrarily, for mere convenience sake” (1859, p. 52). The idea of a species was, for Darwin, relative to the person defining the group. For a recent and interesting take on this discussion see Ereshefsky (2010).
most of the literature surrounding the principle of divergence (and Darwin himself) focuses on the two species that are diverging, the intermediate species are what I find most puzzling. Darwin writes,

...in the diagram I have chosen the extreme species (A), and the nearly extreme species (I), as those which have largely varied, and have given rise to new varieties and species. The other nine species (marked by capital letters) of our original genus, may for a long period continue transmitting unaltered descendants; and this is shown in the diagram by the dotted lines not prolonged far upwards from want of space. (1859, p. 121, my emphasis)

The intermediate species, it appears, have little, if any, variation in their descendants, or if there is any variation it is immediately selected out. It is only species (A) and (I) that produce varieties. Darwin continues, saying “It is worth while to reflect for a moment on the character of the new species F14, which is supposed not to have diverged much in character, but to have retained the form of (F), either unaltered or altered only in a slight degree” (1859, p. 124, my emphasis).

Darwin does not explain why after 14,000 generations, the descendants of species (F) remain unaltered or only altered in a slight degree. He does discuss the possibility of a medium variety persisting, which helps explain why intermediate species can persist:

I am far from thinking that the most divergent varieties will invariably prevail and multiply: a medium form may often long endure, and may or may not produce more than one modified descendant; for natural selection will always act according to the nature of the places which are either unoccupied or not perfectly occupied by other beings; and this will depend on infinitely complex relations. (1859, p. 119)

One could interpret species (F) as having a place in an environment where there are no unoccupied or imperfectly occupied places to seize upon, in which case diverse
descendants would not be advantageous. This would mean, however, that intermediate species like (F) are in static environments where there are no “infinitely complex relations” or, as I will explain in a later section, where there is no real economy of nature, or at least not a dynamic one. In Darwin’s unpublished works, the problem deepens.

1.3 Darwin’s Natural Selection Diagrams

When writing Natural Selection, also known as the Big Species Book written from 1856-1858, Darwin had planned on drawing four diagrams (see Figures 2 and 3).

![Diagram I](image)

Figure 2: Darwin's Diagram I from his unpublished Natural Selection. Darwin is illustrating a pattern of increasing species divergence that results from natural selection for diverse descendants. It is very similar to the diagram he presents in On the Origin of Species except the time axis is flipped, arranged from top to bottom, and none of the intermediate species go extinct.
Figure 3: Darwin’s Diagram II from his unpublished *Natural Selection*. Darwin is illustrating the pattern that results from randomness at each stage instead of from selection for diverse descendants. In the absence of this selection one is to expect neither an increase nor a decrease in species divergence. Below the drawing are Darwin’s notes for Diagrams III and IV that were never completed.

Although he only ever drew the first two, all four are described in the text. They are similar in form to the diagram in the *Origin* except that the time axis is flipped, arranged from top to bottom. In Diagram I (see Figure 2), Darwin illustrates divergence among species (A) and (M) and no extinction or change in the intermediate species “after a vast lapse of time” (1975, cf. p. 244):
In the diagram, A. has given rise to three new species, & M to one. The other species of the genus, B to L, are supposed to have transmitted unaltered descendants [sic]. Hence, even supposing that A & M have been supplanted as I believe will usually have been the case, by their modified & improved descendants, the genus will have become not only more divergent in character (a10 more aquatic than A; & m10 more drought-enduring than M.) but numerically larger. (1975, p. 244-5, my emphasis)

Diagram II is much different from Darwin’s other drawings. Here Darwin presents the expected pattern in the absence of selection for diverse descendants, that is, the pattern that results from randomness with respect to which organisms or varieties survive:

A glance at Diagram 2…everything is the same as in diagram I…except that it is left to mere chance in each stage of descent…[which] varieties are preserved; & the result is, graphically shown, that a10 [sic] & l10 differ in this respect; & so in other respects, hardly more than did the first varieties (a1 l1) which were produced.1 (1975, p. 244, my emphasis)

After 10,000 generations there is no divergence among species. Because of the removal of selection, a notion of relative adaptedness is no longer meaningful. Species (A) and (M) still produce varieties, however, it is no longer the most divergent of them that survive. According to Janet Browne, while writing Natural Selection Darwin believed that “if a ‘fertile’ genus produces more and more species, these species will merely remain variations on a single theme unless divergence intervenes” (1980, p. 88). In Diagram II the varieties produced by the ‘fertile’ species (A) remain “on a single theme” when there is no selection for diverse descendants. The intermediate species show no

4 Because it is outside the scope of this discussion, I merely mention that by “left to mere chance” Darwin does not mean objective chance, but rather “non-fortuitous” chance in the sense of non-correlative. See Hodge (1987) for a more comprehensive explanation.
change with the removal of selection because they do not produce varieties and thus no selection for divergence can ever occur.

Diagrams III and IV were never completed, however, Darwin did provide notes about the drawings (see the bottom of Figure 3) and he does discuss them in the text. Both drawings are variations on Diagram I. Diagram III shows the further divergence of species (M) after a greater lapse of time and Diagram IV represents the passage of even more time and the extinction of the intermediate species except for species (E) and (F):

Continue this process, & all, or nearly all the original species (A to M) will become extinct. In Diagram IV. this is represented, E & F alone now having descendents [sic], whether or not modified. And the final result will be, that we shall have two large groups of modified descendants, coming from the two species, generally the extreme species, (A & M) of the original genus, and differing as much as natural selection could make them from each other & from their two parents, which at the first start differed much: assuredly these two new groups of new species would be ranked in different genera, which would be very distinct, if all the original intermediate species from B to L. had been exterminated, but somewhat less distinct if some of these species (as represented in Diagram iv.) had left descendents, whether or not modified. (1975, p. 246, my emphasis)

Had Darwin drawn Diagram IV it would probably look very similar to the Origin diagram, except that there are two intermediate species (instead of just one) that transmit unaltered or slightly altered descendants. These two intermediate species, (E) and (F), are right next to each other and do not appear to compete with each other or diverge at all. Why do the intermediate species (E) and (F) in Diagram IV and species (F) in the Origin diagram remain so unchanged? One possible explanation is that the species do produce diverse descendants and varieties, but Darwin chose not to draw
them because it was not his primary concern. However, about Diagram I, Darwin says that the varieties produced from species (A) represent a “variable stock, & are still exposed to the conditions which made their parents vary” (1859, p. 242), which is not the case with species (M). This difference is represented by the different patterns of dots under the different species. Thus, the different numbers of dots under different species represent the fact that diverse descendants are only produced under certain conditions, and intermediate species are not exposed to these conditions.

A second possible explanation for why intermediate species appear unvarying is that the variation among descendants is inconsequential and selected out before varieties can ever form. The argument would be that variation arises, but does not accumulate via selection; therefore, Darwin saw no need to draw it. So, for example, species (E) and (F) are kept constant because of a type of stabilizing selection. However, Darwin never says this, and in fact, what he does say many times is that competition between species of the same genus is more severe than species of distinct genera (1859, p. 76). This leads to the conclusion that we should expect species close together in morphological form to diverge, especially if variation is available to be selected. If diverse descendants have the most progeny on average, as stipulated by the principle of divergence (1859, cf. pp. 112, 119), then it must be the case that intermediate species are lacking variation among descendants. It is not that variation is arising and not being selected, but that no variation arises. In the next section I discuss why, based on
Darwin’s concept of variation, some species have the possibility for divergence and some do not. Intermediate species that survive in Darwin’s diagrams are not explained by the principle of divergence, nor can they be understood using a theory of relative adaptedness. Instead, they must be understood using a notion of limited perfect adaptedness. These species are fixed in harmony with an unchanging environment.

1.4 Environment in the Origin

For Darwin, a good environment is an environment where diversity is maximized (Gould 2002). One of the main influences of this view was, no doubt, the social and political economics of the time. Many scholars have thoroughly researched this idea, convicingly, so I merely mention it (for a detailed account see Schweber 1980). Another important influence of this view, often overlooked, is the concept of an economy of nature (Pearce 2010). In an economy of nature, organisms have different structures and habits such that they can specialize and take on different roles. As Pearce notes, Milne-Edwards’ work on physiological division of labor in animals was essential for the principle of divergence: “Darwin saw a parallel between this tendency of parts to take on diverse roles in the animal economy and the tendency of species to diverge into new places in the economy of nature” (2010, p. 515). Darwin writes,

The advantage of diversification in the inhabitants of the same region is, in fact, the same as that of the physiological division of labour in the organs of the same individual body—a subject so well elucidated by Milne Edwards. No physiologist doubts that a stomach by being adapted to digest vegetable matter alone, or flesh alone, draws most nutriment from these substances. So in the general economy of any land, the more widely and perfectly the animals and plants are diversified for
different habits of life, so will a greater number of individuals be capable of there supporting themselves. (1859, pp. 115-16)

In the third edition of the *Origin* Darwin adds a number of sentences also discussing specialization along with division of labor. A definition of the principle of divergence, if we grant Darwin one, is that “…the more diversified in structure the descendants from any one species can be rendered, the more places they will be enabled to seize on, and the more their modified progeny will increase” (1859, p. 119). By diversifying and seizing a new place in the economy of nature, an organism can specialize and use new and different resources for which there may not already be a strong demand (cf. Mayr 1992; Gould 2002; Baker 2005). Darwin goes on to say “natural selection will always act according to the nature of the places which are either unoccupied or not perfectly occupied by other beings; and this will depend on infinitely complex relations” (1859, p. 119). As Pearce points out then, “the possibilities for divergence at any given time are dependent on the state of the economy of nature at that time” (Pearce 2010, p. 518); hence, divergence can only occur if there are places for organisms to occupy. Building on Pearce’s ideas, I contend that there are three different environments found in Darwin’s *Origin* diagram, two include divergence, and one does not.

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For example, see in the Variorum, pp. 221; 382.8:c, 547; 193.1:c; and 222; 382.ii:c (Darwin and Peckham 1959), where Darwin talks about specialization for different functions, specialization of parts and organs, and the accumulation of variations tending toward specialization, respectively.
There are two ways that the process of divergence can interact with the economy of nature (Pearce 2010). First, when there is a diverse environment and complex interactions, there are many unoccupied places to fill. In this case, “the economy of nature is an external constraint on divergence, in that it constrains the possible paths that the latter can take” (Pearce 2010, p. 518). In other words, there will be divergence into the unoccupied places in nature that are bounded by occupied places. Second, when there is an environment that has pre-existing organization, there are many places already filled, though not perfectly. In this case, divergence invades the filled places or creates new places by altering the economy of nature. From both these cases it is clear that “Divergence is dependent on the economy of nature, even though that economy of nature is itself continually modified by divergence” (Pearce 2010, p. 518). Both of these environments are represented in Darwin’s diagrams, I have labeled them environments 1 and 2, respectively (see the triangles labeled ‘1’ and ‘2’ in Figures 4-6).

Triangle 1 in Figure 4 represents divergence into a dynamic economy of nature, where there is a diverse environment and many new places to occupy. In this case the environment or economy of nature is a constraint and determines the new places into which divergence can occur. Diverse organisms compete to fill these new places. Triangle 2 represents an environment with pre-existing organization. Divergence increases competition for already filled places, creating a dynamic and changing environment, as well as creating new places to occupy. In this case divergence alters the
economy of nature. Diverging organisms compete with each other and with the organisms currently filling those places.

Figure 4: The three different environments in Darwin’s *Origin* diagram. The first triangle (1) represents divergence into a dynamic economy of nature where there are new places to occupy, the second triangle (2) represents divergence into an environment with pre-existing organization where divergence increases competition for already filled places, and the third triangle (3) represents an environment without divergence or competition. The first two environments require a concept of relative adaptedness; the third environment requires a concept of limited perfect adaptedness.
To understand the environments represented by triangles 1 and 2 in Figure 4, a concept of relative adaptedness or relative engineering fitness is necessary. Recall that Ospovat defined relative adaptedness by saying, “the adaptedness of every species is relative to the adaptedness of every other species” (1981, p. 206). In environments 1 and 2, diverse organisms compete in a dynamic environment and those that are better adapted to a “real environmental challenge” (Burian 1983), survive.

In the environment labeled by triangle 3, on the other hand, no competition is occurring among species. Species are well adapted to their environment and no variation arises among descendants. Eventually the environment represented by triangle 3 will be replaced by the environment represented by triangle 2 because the descendants of those species will ultimately seize on those places that were “not so perfectly occupied as might be” (1859, p. 102). Prior to this, however, the environment labeled by triangle 3 is best understood using a notion of limited perfect adaptedness. In this environment there is no variation, no competition, and no economy of nature, at least as typically understood, since “For Darwin, as for Lyell, the economy of nature is dynamic and subject to infinitely complex interactions” (Pearce 2010, p. 518). The intermediate species identified by triangle 3 represent species that are well adapted to an

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6 It may be a bit strong to say that absolutely no variation arises among descendants, perhaps it is best to add the disclaimer that there could be a small amount of variation occurring; however, if any variation arose it would not be advantageous because there are no places that diverse descendants can occupy. On the whole I do not think Darwin considered variation either arising at all or arising in a meaningful way in the environment labeled by triangle 3. I will explain why in the section titled “Limited Perfect Adaptedness.”
environment that is not changing, and "having no need to accommodate, do not vary"

Figure 5: The three different environments in Darwin's Diagram I from the unpublished *Natural Selection*. The first triangle (1) represents divergence into a dynamic economy of nature where there are new places to occupy, the second triangle (2) represents divergence into an environment with pre-existing organization where divergence increases competition for already filled places, and the third triangle (3) represents an environment without divergence or competition. The first two environments require a concept of relative adaptedness; the third environment requires a concept of limited perfect adaptedness.

The three environments distinguished in Darwin’s *Origin* diagram can also be found in his unpublished Diagram I (see Figure 5), the only difference being that the third environment is more unchanging. The intermediate species are all supposed to leave unaltered descendants, since the places they occupy are not being invaded and
they are not yet extinct. Darwin’s Diagram II shows only two environments, since there is no selection occurring and the survival of varieties is “left to mere chance” (see Figure 6). The first environment (1*) is dynamic with many new places to occupy, and the second environment (3) is unchanging with no variation.

![Diagram II](image)

**Figure 6:** The two different environments in Darwin’s Diagram II from the unpublished *Natural Selection* representing the absence of selection for divergence. The first box (1*) shows variants that survive by chance and thus divergence does not occur. This environment is dynamic with new places to fill, but diverse descendants are not selected. It is a modified version of triangles 1 and 2 from Figures 4 and 5. The environment on the right (3, which corresponds to triangle 3 in Figures 4 and 5) has no competition or divergence. Neither environment requires a concept of relative adaptedness.

The second environment (3) is like triangle 3 in Figures 4 and 5, but the first environment (1*) is a modified version of the environments represented by triangles 1
and 2 in Figures 4 and 5. Although there is a dynamic economy of nature with new places to fill in the environment labeled by box 1*, the variants that would occupy these places are not selected. The variants that survive by chance do not occupy new places or compete to occupy those places that are not perfectly filled. Instead, these variations remain “on a single theme” as Browne said. No concept of relative adaptedness is necessary for understanding the environment represented by box 1* because there is no selection or sense of being better adapted, and there is no need for a concept of relative adaptedness in triangle 3 for the same reasons as earlier, there is no variation or competition.

I detail the three environments found in Darwin’s *Origin* diagram and unpublished Diagram I in Table 1, which corresponds to Figures 4 and 5.

**Table 1: The three different environments represented in Darwin’s *Origin* diagram and unpublished Diagram I. Table corresponds to Figures 4 and 5.**

<table>
<thead>
<tr>
<th>Environment 1</th>
<th>Environment 2</th>
<th>Environment 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dynamic with changing, complex interactions</td>
<td>Dynamic with pre-existing organization</td>
<td>Static with pre-existing organization</td>
</tr>
<tr>
<td>New places to occupy</td>
<td>Filled places to disrupt</td>
<td>Places not relevant</td>
</tr>
<tr>
<td>Divergence constrained by the economy of nature</td>
<td>Divergence alters the economy of nature</td>
<td>Static economy of nature (if one at all)</td>
</tr>
<tr>
<td>Lots of variation</td>
<td>Increasing variation</td>
<td>No variation</td>
</tr>
<tr>
<td>Relative adaptedness and change</td>
<td>Relative adaptedness and change</td>
<td>Reminiscent of limited perfect adaptedness</td>
</tr>
</tbody>
</table>
Darwin’s principle of divergence discussion in the *Origin* is mostly confined to the first environment detailed in Table 1. The most diverse descendants are selected so that they can occupy new places in a dynamic economy of nature. Environment 2 is mentioned a few times when Darwin states that diverse descendants can invade and seize upon places that are not perfectly filled. The third type of environment, however, Darwin says very little about because it has little relevance to the principle of divergence. The remaining question is why divergence only occurs among the outermost species and why this third type of environment, which requires a notion of limited perfect adaptedness, is part of Darwin’s diagram at all. Divergence can invade new areas or alter old ones, so why, in Darwin’s diagram, do only extreme species diverge?

### 1.5 Limited Perfect Adaptedness

The reason that the intermediate species in Darwin’s diagrams do not diverge is explained by two related ideas: the extremeness and the size of a species. With respect to the first point, Darwin says in the *Origin* that

> In each genus, *the species, which are already extremely different in character*, will generally tend to produce the greatest number of modified descendants; for these will have the best chance of filling new and widely different places in the polity of nature: hence in the diagram I have chosen the *extreme species* (A), and the nearly extreme species (I), as those which have largely varied, and have given rise to new varieties and species. *The other nine species (marked by capital letters) of our original genus, may for a long period continue transmitting unaltered descendants*; and this is shown in the diagram by the dotted lines not prolonged far upwards from want of space. (1859, p. 53, my emphasis)
Species (A) is an extreme species, one that is very different in character from the other species. In *Natural Selection* Darwin makes this point more explicit, asking the reader to “suppose A the most moisture-loving & M the least moisture-loving species” (1975, p. 239). These extreme species occupy extreme environments. To expand on Darwin’s example, species (A) is in an extremely wet environment with other extreme organisms that have adapted to love moisture. The diversity of organisms in an extreme environment leads to “complex interactions” in the economy of nature, and the possibility of new places to occupy. A second and more important point is that an extreme environment has more diverse physical conditions (such as lots of rain or lots of grass), and this is one of the main causes of variation (cf. Darwin 1859, chapter 2; Vorzimmer 1970, pp. 12-13 and chapter 4). Vorzimmer interprets five causes of variation in Darwin’s writings, two of which are the result of physical variation: 1) The Direct Effect of the Conditions of Life and 2) The Indirect Effect of the Conditions of Life. Variation caused by direct effect is based on the male and female reproductive systems, which have somehow been affected during the adult’s lifetime (usually through an environmental stimulus), causing their offspring to vary. The second relevant type of variation—caused by indirect effect—is based on the idea that variation is produced by a particular environmental factor or stimulus such as heat, moisture, light or food (Vorzimmer 1970, see chapter 2).
An extreme species is more likely to produce diverse descendants because of diverse physical conditions. These descendants, being produced in a diverse environment, will have even more diverse or extreme places to seize on, thus causing the next generation of descendants to be diverse as well, and so on. This is why the edges of Darwin’s diagram fan outward, like a driven trend of increasing species diversity. Darwin says “Where many species of a genus have been formed through variation, circumstances have been favourable for variation; and hence we might expect that the circumstances would generally be still favourable to variation” (1859, p. 55). This is also apparent in Darwin’s unpublished Diagram II, where, even though the most diverse varieties are no longer being selected, they are still being produced from the inevitable variation that arises in diverse conditions and extreme environments. Likewise, no variation arises among the species in non-extreme environments. First reason intermediate species do not diverge: Divergence requires variation, variation is dependent on extreme conditions, only extreme species inhabit environments with extreme conditions, thus, only extreme species diverge.

The second reason that intermediate species do not diverge is because they do not contain many individuals, that is, their populations are small in size. Related to the first point is the fact that species only become extreme by inhabiting an extreme environment, and this usually requires a species to be large. Large species cover more area and are more widely distributed causing the descendants of such species to be
exposed to many new and different environments. Darwin says in chapter two that “Alph. De Candolle and others have shown that plants which have very wide ranges generally present varieties; and this might have been expected, as they become exposed to diverse physical conditions…” (1859, p. 53). When introducing his diagram in the *Origin*, Darwin says that the species in the diagram come from a large genus, since “more of the species of large genera vary than of small genera” and that “species, which are the commonest and the most widely-diffused, vary more than rare species with restricted ranges” (1859, p. 117). Species (A) is “a common, widely-diffused, and varying species” (1859, p. 117) and “We have seen that it is the common, the widely-diffused, and widely-ranging species, belonging to the larger genera, which vary most” (1859, p. 128). Because species (A) is large, it means that it has covered, and will continue to cover, many new and different environments, assuring that there will be more variation among descendants and that there will be places to seize upon. It is in this way that divergence continues.7 Second reason intermediate species do not diverge (similar to the first): Divergence requires variation, variation is dependent on extreme conditions, (usually) large species inhabit environments with extreme conditions, thus, (usually) large species diverge.

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7 In *Natural Selection* Darwin says, “Any of the species may vary; but it will generally be those species which are most numerous in individuals & most diffused; & this shows that such species have already some advantages over the other inhabitants of the country” (1975, p. 239, my emphasis). I assume the reason any of the species may vary is conditional on the environment, and if any of the species were in an extreme environment they would vary, and it is most likely that the larger species will cover diverse and extreme environments, causing a species to vary.
Species that are extreme and large will diverge, however, the point about size is weaker than the point about extremeness. If a species in an extreme environment is hit by disaster, decreasing its size by half, it can still diverge, assuming the remaining members are left in extreme environments and the disaster did not much alter the economy of nature. The opposite is not true. If a larger species for some reason only covered many temperate environments, divergence would not occur. The requirement that a species must be large in population size is conditional on the fact that usually a large size or range means the species will cover extreme environments. The common factor with both reasons, extremeness and size, is that an extreme environment is necessary. If we look at the intermediate species (F) in the Origin diagram, it is neither extreme, nor very large, and if it became large it would likely only cover more temperate environments. Thus, the only way for species (F) to diverge is if the environment changes and becomes more extreme. Even something as simple as a change in the amount of food available could cause variation to arise among the descendants of (F). As Ospovat says, “In 1844 an increase in food is allowed to be perhaps a minor cause of variation; in Natural Selection it is said to be an important cause; and by 1868 Darwin called it probably the single most powerful cause” (1981, p. 208). In sum, an environmental shift must occur for (enough) variation to arise, varieties to be produced, and divergence to take place, that is, the environment must become more extreme. This precondition for divergence mirrors the idea of limited perfect adaptedness.
Intermediate species remain the same and transmit unaltered descendants unless there is an environmental change from a physical cause (e.g. weather shift) or from invasive (diverging) organisms altering the environment. At least one of these changes would be necessary for intermediate species to break their previously “harmonious molds.”

1.6 The Pattern in Darwin’s Diagram

Darwin’s principle of divergence and views on variation are mostly considered incorrect by today’s standards; however, environments 1 and 2 in Darwin’s diagrams are consistent with the conventional wisdom of how diversity increases. Various authors have argued that species divergence has increased over macroevolutionary time (Foote 1996; Gavrilets 1999; Ciampaglio et al. 2001; Pie and Weitz 2005; Erwin 2007) and the fact that animal life has diversified over the Phanerozoic Eon is “arguably the best known and most widely acknowledged pattern in macroevolution” (McShea and Brandon 2010, p. 34). Explanations for this increase in diversity vary, however, Darwin’s idea that organisms expand into new environments is usually a factor (McShea and Brandon 2010, p. 34 and see pp. 36-7). For example, Novack-Gottshall (2007) and Bambach and colleagues (2007) appeal to the invasion of new habitats to explain species

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8 I should make explicit the fact that a theory of limited perfect adaptedness on the whole refers to the harmony of an organism with its environment, and here I am making the claim that intermediate species are in harmony with their environment. However, I do not think this presents any problems since Darwin was not arguing for species-level selection. Species divergence is explained by selection on the diverse organisms that make up the species (or variety). Thus I could have said that “a species of intermediate organisms” instead of “an intermediate species” is in harmony with its environment until the environment is altered.
divergence, and McShea and Brandon (2010) complement this view by demonstrating that species which seize new habitats change randomly with respect to each other. This phenomenon, known as the Zero Force Evolutionary Law (hereafter, ZFEL), produces a trend of increasing variance among species that looks similar to the pattern of macroevolutionary divergence seen in Darwin’s *Origin* diagram. However, as I will explain in more detail in the next section, the ZFEL does not predict a pattern like species (F) or the pattern in Diagram II where the absence of selection results in no change among species. For Darwin, stasis was to be expected in environments where there was no variation or selection, but this is incorrect, we should instead “…see stasis as a strong signal of selection…” or more generally as the result of strong evolutionary forces (McShea and Brandon 2010, p. 119). Thus, species (F) and the unchanging pattern in Diagram II can be explained by stabilizing selection. For Darwin, the intermediate species in environment 3 were merely the background and the divergent species in environments 1 and 2 the foreground; however, as Gould and Eldredge said in reference to their famous theory of punctuated equilibrium, “stasis is data” (1993, p. 223).

1.7 Zero Force Evolutionary Law

While the rest of this dissertation will discuss the implications of the ZFEL in great detail, this section will introduce the law by illustrating how it can clarify Darwin’s principle of divergence, specifically his *Origin* diagram. In brief, the ZFEL is a biological law that makes a claim about evolutionary systems in the absence of selection and
constraints. Whereas Darwin’s expectation in the absence of selection was stasis, the ZFEL makes the claim that given an evolutionary system with variation and heredity, in the absence of selective forces and constraints, the expectation is an increase in variance among entities. To put it in Darwin’s framework, the ZFEL null expectation is an increase in diversity, specifically, species diversity. Thus, the pattern in Darwin’s diagram is expected. According to the ZFEL, it is not necessary to explain this pattern using a selective explanation such as selection for extreme or divergent species and varieties.

Why does the ZFEL predict an increase in species diversity? The answer is because, absent selection and constraints, species are all varying randomly with respect to one another. For example, suppose there are six species, all in different environments. Each species is varying and changing and adapting to its specific environment; however, because all six species are changing randomly with respect to one another (that is, there is no selection or constraints affecting the group of those six species), the variance or diversity of all six species is expected to increase. This can be seen in Figure 7, reproduced from McShea and Brandon (2010, p. 15), where the particles can be interpreted as changing species. The resultant pattern is an overall trend of macroevolutionary divergence that did not require selection, yet looks very similar to Darwin’s Origin diagram. As McShea and Brandon explain, selection can still be part of the divergence story, but not in the way that Darwin thought:
The basic form of our argument is this: to the extent that different lineages exploit different opportunities, use different resources, adopt different strategies, and so on, changes among lineages will be independent of each other, and therefore the divergence among them is a consequence of the ZFEL. Suppose that one clade of clams evolves a streamlined shape to burrow more effectively into soft mud. And another evolves an acid-producing gland to burrow into hard coral. The resulting phenotypic divergence is the ZFEL. Notice that selection is involved. In this story, it drives adaptive change in both lineages. But the selective forces are somewhat different in each lineage, so that lineages change to some degree randomly with respect to each other. And as a result, they become ever more different from each other, more disparate, with time. Selection is involved, but—and this is critical—not selection for divergence. That would not be the ZFEL. (2010, p. 34)

![Figure 7: The increase of variance over time in an ensemble of six particles. Reproduced from McShea and Brandon (2010, p. 15)](image)

Darwin’s principle of divergence can be correct in the sense that there is “adaptation in individual lineages to exploit new opportunities”, but, as Brandon and McShea go on to explain, it is “occurring to some degree differently in each species and producing an expansion into unoccupied ecospace” (2010, pp. 36-7). Within the ZFEL framework, environments are always changing, there is always variation, and there are always new
opportunities to exploit since organisms are never “perfectly adapted.”

Returning to Darwin’s three environments with a new ZFEL perspective, we can now interpret them differently (see Table 2). In Environments 1 and 2, individual varieties and species are exploiting new opportunities or places in the economy of nature. These lineages are adapting to these new places randomly with respect to each other, i.e., divergence is occurring. There is selection at the organismic level for adapting to new environments, and there may also be selection at the species level for divergent species, however, whether or not there is selection at the species level does not change that fact that the ZFEL still holds. There is always the tendency for variation to increase and there is always the tendency for species to diverge, whether or not there is also selection aiding that ZFEL tendency for divergence.

**Table 2: The three environments in Darwin's *Origin* diagram, reinterpreted with the Zero Force Evolutionary Law as inspiration.**

<table>
<thead>
<tr>
<th>Environment 1</th>
<th>Environment 2</th>
<th>Environment 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual lineages are exploiting new opportunities</td>
<td>Individual lineages are exploiting new opportunities</td>
<td>Individual lineages are kept stable by stabilizing selection and constraints</td>
</tr>
<tr>
<td>Species vary randomly with respect to each other, causing divergence</td>
<td>Species vary randomly with respect to each other, causing divergence</td>
<td>Species are not varying, thus divergence does not occur</td>
</tr>
<tr>
<td>Selection for divergence may be occurring</td>
<td>Selection for divergence may be occurring</td>
<td>Selection for stability is occurring</td>
</tr>
<tr>
<td>The ZFEL is acting</td>
<td>The ZFEL is acting</td>
<td>The ZFEL is acting</td>
</tr>
</tbody>
</table>
The static nature of Environment 3 is now explained by strong stabilizing selection or constraints opposing the ZFEL tendency such that species do not vary and divergence does not occur. Just because there is no divergence or an increase in diversity in Environment 3 does not mean the ZFEL is no longer acting, it is simply being opposed. Similarly, in Darwin’s unpublished diagram II, the interpretation is now that there is strong selection on all lineages, causing them to stop varying and diverging with respect to each other. Darwin was trying to show in diagram II the pattern that would result in the absence of selection for diverse descendants, however, what he really showed was a pattern that required selection.

The ZFEL explains the natural or background condition of evolving populations and organisms, where “change is the result of a new opportunity, genetic or environmental, a novel adaptation or the opening of new ecospace, or both. And that opportunity is exploited to some degree differently by each lineage. The result is divergence. And that is the ZFEL” (McShea and Brandon 2010, p. 37-8).

1.8 Conclusion

Darwin said in Natural Selection that his diagram “will, also, clearly show several points of doubt & difficulty” (1975, pp. 238-9), and perhaps he is referring to the fact that his diagram represents the transition from a view of limited perfect adaptedness to a view of relative adaptedness. As Janet Browne says,

Darwin’s theories changed and evolved as he himself grew older and more mature, and that the "Essay" and Natural Selection - and indeed, the Origin as well - represent
only his considered opinion on the problem of species at a given point in time. There is no good reason to believe that Darwin's ideas were static from the "Essay" onward… (1980, p. 89)

I argue his ideas were not static and that his diagram represents the shift from the view in the “Sketch of 1842” and the “Essay of 1844” that variation in nature is rare, to the view held throughout most of the *Origin* that variation is ubiquitous. The latter view is clearly the driving force in his discussion and understanding of the principle of divergence; however, the former view is still part of his diagram. Intermediate species, specifically species (F), leave unmodified or only slightly modified descendants after long spans of time. This is explained by the fact that intermediate species are well adapted to temperate environments where variation does not arise. Without any changes in the environment, intermediate species continue to transmit unaltered descendants that are in harmony with their environment. This is the idea of limited perfect adaptedness, and it is necessary for understanding why the intermediate species in Darwin’s diagram do not diverge like the outermost species, which inhabit extreme, dynamic environments.

If we imagine Darwin’s diagram after many more generations, there will only be divergent species and extreme environments. The original intermediate species in temperate environments will be replaced by invasive diverging species from more extreme environments. This is much like Darwin’s idea of relative adaptedness slowly invading and replacing his previous belief in limited perfect adaptedness until it too
disappears. Eventually, Darwin gave up the belief that variation in nature is rare and that stasis is always the null expectation, but at the time he drew the diagram in the *Origin*, it still persisted, unaltered, seen most clearly in that intermediate species (F).

In the following chapters I investigate the Zero Force Evolutionary Law in greater detail with respect to many current issues in biology and philosophy of biology. While this chapter illustrated the fact that the ZFEL framework can be applied to historical evolutionary explanations, the rest of the dissertation will illustrate a variety of ways that the ZFEL framework can be applied to modern day evolutionary research.
2. Network Theory and the Formation of Groups without Evolutionary Forces

Biology is hierarchically structured. It depends on the formation of groups—groups of molecules make up cells, groups of cells make up organisms, and groups of organisms make up societies. The initial formation of a group poses a problem because it introduces a conflict between levels; why would entities, capable of independent replication, forego that advantage to replicate only as part of a group? Although a very common question, perhaps one of the most well-known places it is found is in Maynard Smith and Szathmáry’s *The Major Transitions in Evolution* (1995), demonstrating how the question of group formation is inextricably linked to questions about hierarchy.

Maynard Smith and Szathmáry, along with many others (e.g. Buss 1987; Okasha 2006; Grosberg and Strathmann 2007), focus almost exclusively on adaptive explanations, that is, questions about the formation of groups are posed assuming the presence of evolutionary forces, in particular, natural selection.

The aim of this project is to investigate the possibility of group formation in the absence of evolutionary forces. In this chapter, as in most of the evolutionary transitions literature, groups are understood very generally as collections of entities at any level of organization. This is similar to Peter Godfrey-Smith’s “Darwinian Populations” concept, except that his focus is on how collections of things can change via natural
The inspiration for this investigation is the Zero Force Evolutionary Law (ZFEL), which, stated generally, says:

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, and constraints acting on diversity or complexity. (McShea and Brandon 2010, p. 4)

Diversity is defined as “a function of the amount of variation among individuals” (p. 2) and complexity, similarly, as “a function only of the amount of differentiation among parts within an individual” (p. 2). Although “diversity” is defined in the standard way, “complexity” is more technical in this context than its colloquial usage, which incorporates function. Diversity and complexity are the same measure, except that complexity is one level up, so diversity at level n is complexity at level n+1. These measures apply to all levels of biological hierarchy, not just to an individual organism and its parts. The ZFEL can also be stated in a special or zero-force formulation, which says that in the absence of forces and constraints, diversity and complexity are expected to increase. An important point to stress is that the ZFEL describes the phenomenon of increasing variance, and the causes of this phenomenon are many. Thus, a possible cause of variation, such as genetic drift, should not be conflated with the ZFEL; the former describes a cause, the latter a phenomenon.

The reason that variance is expected to increase is based on the fact that entities are differing randomly with respect to each other. One way to understand this is by thinking about a picket fence recently painted white so that each picket is identical at the
start (McShea and Brandon 2010, pp. 2-3). As time passes the pickets begin to vary, one gets peed on by a dog, another gets hit by a piece of hail, another gets stained by a dandelion, and so on. Because all of the pickets are varying randomly with respect to each other, the variation among the pickets has increased, that is, the complexity of the entire fence (n+1) or the diversity of the pickets (n) has increased. As McShea and Brandon say, “No directed forces need to be invoked here…diversity and complexity arise by simple accumulation of accidents, producing a steady, background increasing tendency” (2010, p. 3). The background expectation is change, that is, increasing variation.

To model this background tendency for increasing variation among entities, network theory was most appropriate because network models study the formation, behaviors and patterns of relations. In a network, entities are represented as nodes and the connections they form as edges (see Figure 8). Despite the prevalence of modeling and mathematics in the literature pertaining to the origin of groups and biological hierarchy, one area that seems to have been overlooked is network theory. Networks have been used in biology to investigate empirical findings in biochemical, molecular, cellular, neuronal, organismal and ecosystem contexts, among others (Alon 2003; Fewell 2003; Laughlin and Sejnowski 2003; Lusseau 2003; McAdams and Shapiro 2003; Croft et al. 2007; Bascompte 2009; Franks et al. 2009; Godfrey et al. 2009; Henzi et al. 2009; Krause et al. 2009; Naug 2009; Ramos-Fernández et al. 2009; Sih et al. 2009). However, biology has yet to use network models theoretically for studying the formation of groups.
Figure 8: An example network with eight nodes connected by nine edges. There is also one unconnected node.

This chapter presents a modified random network model to illustrate how groups can form in the absence of evolutionary forces. Random networks, or random-graph models of networks, are more about answering the how questions as opposed to the why: how do certain networks form, how do they behave under certain modifications, and for this project, how can groups form spontaneously? The Erdős-Rényi random graph model, introduced by Paul Erdős and Alfréd Rényi, is a model where nodes are connected randomly. Edges form independently from each other, based on a set probability; so between any two nodes there is an equal probability of an edge forming. One of the characteristics of a purely random model is the suddenness with which the network becomes highly or maximally connected (Albert and Barabási 2002). This
prevents the formation of isolated subgraphs or groups. The model presented in this chapter, hereafter called the **ZFEL model**, includes the following two assumptions that a purely random network does not: The first (1) is that nodes are dynamic. They have a tendency to change as time passes, and nodes change independently of each other. Hence, the variation among nodes increases over time. The second assumption (2) is that edge formation is determined by node variation. Only nodes that have changed can form edges with other nodes, meaning two unchanged nodes can never form an edge (although a changed node can form an edge with an unchanged node). As node heterogeneity increases over time, the probability that edges will form increases as well. I show that, when modeled, the ZFEL expectation of increasing variation results not only in the formation of groups, but also in a higher probability of group formation than is found in a model that is purely random.

### 2.1 The ZFEL Model

The first assumption, that nodes are dynamic, comes directly from the description of the Zero Force Evolutionary Law, which, as was quoted in the introduction, says that variation among entities (nodes) is expected to increase as time passes. The second assumption, that edge formation is determined by node variation, is derivative of the ZFEL. Implicit in this assumption is the idea that each edge that forms

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1 This is often referred to in the graph theory and network literature as a clustering coefficient, and random networks are known for their extremely low clustering coefficients.
is a different type. In the random model, nodes are homogeneous so any edge that forms will be the same type (because it is between the same types of nodes), however, in the ZFEL model, every edge that forms is a different type because it is connecting a different set of nodes. The basic idea is this: As the variation among entities grows, so does the range of possible interaction types between those entities. As an example, imagine a group of homogeneous entities such as 28-year-old graduate students that have a limited range of association types among them. If one of the 28-year old graduate students changes by becoming, say, a professor, there is now the possibility for novel (new types of) interactions between the professor and the other graduate students; hence, a changed entity (node) is capable of behaviors or connections (edge formations) the other unchanged entities alone are not. As the number of possible connections (and possible novel connections) increases, so then does the probability that an actual connection will occur, and eventually these actual connections will lead to the formation of a group. This theory of self-organization is not new; in fact, Stuart Kauffman makes a rather similar point with respect to molecules (1993, pp. 348-50; 1995, p. 62). To understand this self-organization at the biological level, a few examples are helpful.

First, consider the evolution of sex. There is still much controversy surrounding how and why sexual reproduction developed, and these issues are beyond the scope of this discussion; however, for the sake of illustration, imagine a population of single-celled organisms like protozoa. These organisms are asexual and haploid and have
limited interactions with each other. Over time these organisms start to vary (the first assumption of the ZFEL model). Perhaps some become diploid by fusion and some become diploid by endomitosis. New types of interactions are now possible between the original haploid organisms and the new diploid organisms, and there are novel interactions possible between the new diploid organisms. Eventually the haploid-diploid cycle of reproduction is born (Michod 1995, p. 144). It has even been shown that in a heterogeneous group including sexual and asexual reproducers and haploids and diploids, the diploid sexual reproducers will eventually take over the population because of the defense gained against too many deleterious mutations (Jan et al. 2000; Örçal et al. 2000; Tüzel et al. 2001; Tüzel et al. 2001). Whether or not this is true is not relevant to this discussion, however, the important point is that variation must have first increased among organisms such that new types of interactions could form, leading to the production of new groups, in this case, groups of sexual organisms.

As a second example, think about the evolution of multicellularity. It is likely that multicellularity originated via the aggregation of solitary free-living cells or via cells remaining attached and not separating after mitosis (Bonner 1998). According to Newman and Muller (2000), both of these scenarios can be explained by the advent of cell adhesion. Cells began with uniformly neutral adhesivity; however, through random differentiation they varied and eventually some cells became slightly adhesive and some slightly anti-adhesive. This variation in entities introduced new ways of interacting and
consequently new ways for groups to form. Based on the assumption that these entities move randomly, interactions are likely to occur, specifically, interactions between the cells with more adhesive-type surfaces, resulting in bonds between those cells. This simple mechanism of adhesion, which results from variation and random interaction, can help explain the emergence of multicellular forms.\(^2\)

A third and final example is the evolution of division of labor in complex insect societies. Jeanson, Kukuk, and Fewell (2005) compared solitary and communal halictine bees, the former make individual nests and the latter cooperate to make one common nest, which is easier to guard from predators. Neither the solitary nor the communal halictine bees exhibit division of labor in nature. However, Jeanson and colleagues found that when forced to cohabit, “division of labour within the associations of solitary bees during early nest construction was actually higher than in communal associations” (2005). That is, the solitary halictine bees were more likely to engage in division of labor than the communal halictine bees when cohabitation was forced. They conclude that “the cooperative interactions displayed by the communal bees might prevent the development of a division of labor” (2005, p. 1191) because these bees are selected to be more homogeneous in their behaviors to aid cooperation. Solitary bees, on the other

\(^2\) This example is also useful because it illustrates the point that there can be degrees of connectivity between entities. This is not apparent in the ZFEL model since it is designed such that entities are either connected or they are not. Weighted networks incorporate weighted edges, or different edge strengths, and I hope to address this issue in future research.
hand, vary in their response thresholds or “intrinsic sensitivities” to task stimuli (Page and Mitchell 1991; Page 1997; Fewell and Page 1999; Beshers and Fewell 2001; Jeanson et al. 2005; Nowak et al. 2010). This variation in response thresholds means there are different types of interactions possible between solitary bees that are not possible between communal bees. Page and Mitchell (1990) suggest that this variance in behavior “is central to task organization, and that task specialization within honey bee colonies self-organizes from intrinsic variation among members in their probabilities of performing different tasks.” Thus, in this example, it is clear that variation among individuals results in many different types of interactions, which is necessary for the emergence of complex societies or groups with division of labor.

The three biological examples above highlight three different events in the history of biological hierarchy where group formation was necessary, the evolution of sex, the evolution of multicellularity and the evolution of division of labor or coloniality. I mention each case as support for the second assumption in the ZFEL model that as node heterogeneity increases, so does the range of possible edge types, and thus the possibility of edge formation increases as well. These examples also demonstrate how new types of connections or edge formations lead to the formation of groups, which will be further substantiated by the results in this chapter.
2.2 Methods

Cluster, cycle, and clique subgraphs were considered as a way to investigate the probability of group formation in the ZFEL and random models. They are defined as such: 1) a cluster is a group of nodes in which every two nodes are connected via some sequence of edges, 2) a cycle is a group of nodes that are closed by a sequence of edges, and 2) a clique is a group of nodes that are maximally connected, that is, every node has formed an edge with every other node (cf. Jackson 24, 26, 27-28). Clique formation is highly restrained, meaning that among a specified set of nodes there is only one way that a clique can form (every node forms an edge with every other node), but cycles and clusters have more flexibility. Depending on how one decides to investigate cycles, a cycle can either allow repeated nodes or not allow nodes to appear more than once except for the start/end node. In the latter case each node has exactly two neighbors, but in the former case many different types of cycles can form among a certain set of nodes since nodes can have more than two neighbors. With respect to clusters there is even more variability of expression among a set of nodes since the requirement is “some sequences of edges”; thus, a cluster can form among the same group of nodes in many different ways. See Figure 9 for examples of all three types of subgraphs and see the grey box in Figure 10 for an example of the twelve different ways a cluster can form out of four nodes and two edges. Both Figures are explained in detail in the next section.
2.2.1 Probability of 3-clusters, 3-cycles, and 4-cliques

First, clusters of size three, cycles of size three and cliques of size four were considered (the number refers to the number of nodes, see Figure 9).

![Cluster of Size 3](image1.png) ![Cycle of Size 3](image2.png) ![Clique of Size 4](image3.png)

Figure 9: Example subgraphs where size refers to the number of nodes. A cluster of size three contains three nodes and two edges, a cycle of size three contains three nodes and three edges and a clique of size four contains four nodes and six edges.

The probability of each subgraph forming in the random and ZFEL models was computed using combinatorics, specifically the choose function, i.e., the binomial coefficient \( \binom{n}{x} \) usually read as “n choose x.” It can also be written using factorials:

\[
\binom{n}{x} = \frac{n!}{x!(n-x)!}
\]

The idea behind the choose function is that of \( n \) things, you can choose \( x \) of them in an unordered fashion. For example, if you have a bag of four different colored balls (input 4 for \( n \)) and you want to choose two of them (input 2 for \( x \)), there are six different possible combinations of choosing two balls (remember order doesn’t matter). The choose function was used to calculate the probability of certain groups forming, usually
by choosing the number of edges necessary for a certain subgraph (although it was also used for choosing nodes).

For example, to calculate the probability of a cluster of size 3 (3-cluster) forming in the random model, Eq. (1) divides the number of possible graphs producing a 3-cluster by the total number of possible graphs that can be formed with $n$ nodes and two edges. Specifically, the choose function in Eq. (1) says, given a node, let’s call it node A, two edges need to connect to node A in order to form a cluster. There are $n$-1 number of nodes that node A can attach to and by choosing two of those possible attachments and then multiplying the entire choose function by the number of nodes, the numerator of Eq. (1) is able to represent the number of possible graphs in the random model that can produce a 3-cluster. The denominator of Eq. (1) is also a choose function calculating the number of ways two edges can form in a network of $n$ nodes, that is, the total number of possible graphs that can be formed with two edges and $n$ nodes. To take a specific example, in a network of four nodes, according to the numerator of equation 1, the number of graphs that produce a 3-cluster when two edges are chosen is twelve (see the grey box in Figure 10). The total number of possible graphs that could form given two nodes in a 4-node network is 15 (the denominator of Eq. (1) and the white box in Figure

---

3 This denominator was also used when measuring 3-cycles and 4-cliques, except for changing the number of edges being chosen (see Appendix A for details).
This means the probability that a 3-cluster will form in a 4-node network is $\frac{12}{15}$ or 0.8.

Figure 10: The 15 graphs that can form in a four-node network given two edges. The grey box illustrates the numerator of equation 1, that is, the 12 graphs that form containing a 3-cluster. The surrounding white box represents the denominator of equation 1, that is, the 15 graphs that can form containing two edges. The probability that a 3-cluster will form in a random 4-node network given two edges is $\frac{12}{15}$ or 0.8.

(1) 

$$n \cdot \binom{n-1}{2} = \binom{n(n-1)}{2}$$
Calculating the probability of a 3-cluster forming in the ZFEL model was a bit more difficult because of the restriction that two undifferentiated nodes cannot form an edge. The method of calculation is basically the same where \( n \) is the total number of nodes, however, \( x \) now represents the number of differentiated nodes and the probability of \( n \) choosing \( x \) is conditional on the number of differentiated nodes.

Equation (2) divides the number of possible graphs with a 3-cluster by the total number of possible graphs that can be formed with two edges, taking into account the number of nodes that have differentiated, represented by \( x \). To understand how a cluster can form in the ZFEL model let’s look at three nodes, \( A \), \( B \), and \( C \), where a cluster will have two edges, \( \{A,B\} \) and \( \{B,C\} \). There are three ways a cluster can form in the ZFEL model: 1) all three nodes can be differentiated, 2) any two of the three nodes can be differentiated, or 3) the middle node alone can be differentiated. In the numerator when calculating

\[
x \cdot \binom{x-1}{2}
\]

represents all three nodes as differentiated,

\[
3 \cdot (n-x) \cdot \binom{x}{2}
\]

represents two of the three nodes as differentiated, and the last part of the numerator

\[
x \cdot \binom{n-x}{2}
\]

represents only the middle node, \( node~B \) in this case, as differentiated. Added all together these three parts represent the number of possible graphs in the ZFEL model that can produce a 3-cluster. To represent the total number of possible graphs that can be formed with two edges in the ZFEL model, both the total number of nodes and the number of differentiated nodes must be taken into account. In the denominator, the
fraction in the top part of the choose function can be seen as two different fractions. The first part, \( \frac{n\cdot(n-1)}{2} \), calculates the total number of edges that can be formed, like in Eq. (1), and then subtracted from that is \( \frac{(n-x)\cdot(n-x-1)}{2} \), which represents the edges between undifferentiated nodes that in the ZFEL model cannot form. From this entire fraction, which represents the total number of possible nodes that can form edges in the ZFEL model, two edges are chosen to represent the total number of ways that two edges can form.  

\begin{equation}
\begin{aligned}
(2) \\
&= x \cdot \binom{x-1}{2} + 3 \cdot (n-x) \cdot \binom{x}{2} + x \cdot \binom{n-x}{2} \\
\end{aligned}
\end{equation}

2.2.2 Probability of clusters, cycles, and cliques over time

Second, clusters, cycles and cliques of all sizes were evaluated over time. The ZFEL and random models were simulated using the statistical program R, and measured by using and modifying the functions in the package igraph©. Specifically, 1) the number of edges, 2) the number of clusters, 3) the average cluster size, 4) the average

\footnote{This denominator was also used for measuring 3-cycles and 4-cliques in the ZFEL model, except for changing the number of edges being chosen (see Appendix A for details).}
size of the largest cluster, 5) the average size of the longest cycle 6) the number of cliques, 7) the average clique size, and 8) the size of the longest clique was measured, taking the average from 100 simulation runs. The ZFEL model program used the following four parameters: 1) the number of nodes, 2) the number of generations, 3) the probability that edges form and 4) the probability that nodes change state. The random model was simulated similarly except that it used only the first three parameters and had no restrictions on what edges could form. Nodes were given states in the ZFEL model to represent node variability. At time $T_0$, all nodes started in state 0 and none of the nodes were connected by any edges. At time $T_1$, each node had the same probability of changing its state, that is, if there are five nodes, then all five nodes have the same specified probability of changing to a different state that is not 0, and each state (beyond 0) is unique. So at time $T_1$, the first node to differentiate in the program changes from state 0 to state 1, the second node to differentiate changes from state 0 to state 2, and so on. If a node does not change, it keeps its current state, and if it does change states, its current state is replaced.\(^5\) Node state is important because edges cannot form between two undifferentiated nodes, that is, an edge cannot form between two nodes in a state of 0. Therefore, as node differentiation increases over time, the probability of edges

\(^5\) It is not necessary for each new node state to be unique; this method was just for ease of calculation and evaluation. A different model, where at time $T_1$ differentiated nodes change from state 0 to 1, and then at $T_2$: differentiated nodes change from either state 0 to 1 or 1 to 2, could also be used; however, the results would be the same under both methods because the only real constraint is that edges do not form between two nodes in state 0.
forming increases as well. At hypothetical time \( T_1 \), it is likely that some nodes have changed states, so every node pair that is not \([0,0]\) now has the same specified probability of forming an edge. At time \( T_2 \) nodes can change states again. If a node that formed an edge in \( T_1 \) changes its state in \( T_2 \), the previous edge is now gone. So the rule is, if two nodes that are connected by an edge at time \( T_x \) do not change states at time \( T_{x+1} \), the edge carries over to the next generation. If one of the two nodes does change states, the previous edge is lost, and possibly replaced by a new type of edge or possibly the nodes are left unconnected.\(^6\)

2.3 Results

2.3.1 Probability of 3-clusters, 3-cycles, and 4-cliques

In the random model, given a fixed number of nodes, there is a single probability that a 3-cluster, 3-cycle, or 4-clique will form; however, in the ZFEL model not all nodes can form edges so the probability of group formation depends on the number of differentiated nodes. For that reason the following values for \( x \) (number of differentiated nodes) were measured in a 100-node network: 5, 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100. As Figures 11 and 12 show, when the number of differentiated nodes is

\(^6\) If this is still confusing, consider the following example: At time \( T_8 \) there are four nodes, \( A, B, C, \) and \( D \) in the states \( 0, 5, 3, \) and \( 7, \) respectively. There are also the following edges: \([A,D]\) \([A,C]\) and \([C,B]\). At time \( T_9 \) the four nodes, \( A, B, C, \) and \( D \) are in states \( 0, 5, 8, \) and \( 7, \) respectively. Because node \( C \) changed states, only the edge \([A,D]\) is carried over to \( T_9 \) while every other possible pair of nodes has the same probability of forming a new edge.
less than half the total number of nodes, the probability that a 3-cluster or 3-cycle will form is much higher than in the random model.

Figure 11: The probability that a 3-cluster will form in both the random and ZFEL models. In the ZFEL model the horizontal axis represents the number of nodes that have differentiated. This is important because in the ZFEL model two undifferentiated nodes cannot form an edge. In the random model all nodes can form edges, hence there is no change in probability, it is only used as a baseline.
Figure 12: The probability that a 3-cycle will form in both the random and ZFEL models. In the ZFEL model the horizontal axis represents the number of nodes that have differentiated. This is important because in the ZFEL model two undifferentiated nodes cannot form an edge. In the random model all nodes can form edges, hence there is no change in probability, it is only used as a baseline.

However, as the number of differentiated nodes increases to above half, the ZFEL model basically converges with the random model. Cliques are rather difficult to form because all of the nodes need to connect to all other nodes. In the ZFEL model this means only one node in a clique can be undifferentiated, if there were two, a necessary edge could not form. When the number of differentiated nodes is greater than 10, the probability of a 4-clique forming is much lower than in the random model (see Figure 13); since, in the random model every node has the possibility of forming an edge with every other node.
Whereas this fact was hindering to forming clusters and cycles, it turned out to be helpful when forming cliques.

Figure 13: The probability that a 4-clique will form in both the random and ZFEL models. In the ZFEL model the horizontal axis represents the number of nodes that have differentiated. This is important because in the ZFEL model two undifferentiated nodes cannot form an edge. In the random model all nodes can form edges, hence there is no change in probability, it is only used as a baseline.

2.3.2 Probability of clusters, cycles, and cliques over time

The ZFEL model does not accumulate edges as quickly as the random model, nor does it reach the same threshold. Figure 14 shows the results of a 100-generation simulation with a variety of edge formation probabilities. Both models begin to plateau around the probability 0.05, however, the random network levels out at the maximum
number of edges possible in a 100-node network, 4950, while the ZFEL network lingers around 900 edges. Similarly, Figure 15 shows edge formation over generational time with a set edge formation probability of 0.05, clearly showing how quickly the random model accumulates edges and reaches maximum connectivity compared to ZFEL model.

Figure 14: The number of edges that form on average over different edge formation probabilities in the ZFEL and random network models after 100 generations in a 100-node network. The random model plateaus at the maximum number of edges possible in a 100-node network, 4950. The number of simulation runs was 100.
Figure 15: The number of edges that form on average in the ZFEL and random network models over generational time in a 100-node network. The edge formation probability for both networks is 0.05 and the number of simulation runs was 100.

Measuring clusters in both models over generational time demonstrates that the random network is too connected even after ten generations to have any real group formation. Figures 16, 17, and 18 illustrate this by comparing the average number, average size, and largest size of clusters measured in both models over 1, 10, 25, 50, and 100 generations with an edge formation probability of 0.05. The ZFEL model does reach a state of high connectivity (when the entire network is one big cluster), however, the trend is much slower, allowing for greater production of isolated clusters along the way.
NB: Minimum cluster size is one node, maximum cluster size is 100 nodes (the entire network), and nodes can only be part of one cluster at a time.

Figure 16: The number of clusters that form on average in the ZFEL and random network models over generational time in a 100-node network. The edge formation probability for both networks is 0.05 and the number of simulation runs was 100. If no edges are present the number of clusters is 100, if all nodes are somehow connected the number of clusters is 1.
Figure 17: The average size of clusters that form on average in the ZFEL and random network models over generational time in a 100-node network. Cluster size is calculated based on the number of nodes in a cluster, and the edge formation probability for both networks is 0.05. The number of simulation runs was 100.
Figure 18: The largest cluster to form on average in the ZFEL and random network models over generational time in a 100-node network. Cluster size is calculated based on the number of nodes in a cluster, and the edge formation probability for both networks is 0.05. The number of simulation runs was 100.

Gathering data on cycles and cliques over generational time was difficult because igraph® allows nodes to be in more than one cycle or clique at the same time, meaning those cycles or cliques that were counted were likely not isolated. Because the random model quickly becomes connected, there is little to measure—either there are no subgraphs, or there are so many overlapping subgraphs that the program cannot count their number or type. The ZFEL simulations produced more data than the random model, however, the same difficulties did arise. That data can be found in Appendix A.
Similar to the cluster data, cycles were also found to be more likely to form in the ZFEL rather than random model (see Figure 33 in Appendix A), and cliques of three nodes or more were found to be very unlikely in both models (see Figure 34 and 35 in Appendix A).

2.4 Discussion

The Zero Force Evolutionary Law makes a claim about what to expect in the absence of forces and constraints—an increase in diversity and complexity. As I have shown in this chapter, this zero-force expectation also leads to the expectation of group formation (collections of entities) at every level of biological hierarchy. Put simply, \textit{entity variation makes group formation easier}. This conclusion is not necessarily intuitive. Take, for example, the case of division of labor among insects mentioned in section 2.1. It is not unreasonable to assume a completely selective explanation for the emergence of complex societies: entities were selected to become more cooperative and homogeneous, and groups of these cooperators were selectively favored. Then those cooperative groups with specialized entities, and eventually groups with division of labor, were selected. However, as I pointed out earlier, selection for cooperation and homogeneity seems to have actually inhibited the emergence of division of labor (Jeanson et al. 2005, p. 1191). Variation among entities, which results in new and different types of interactions, is necessary for complex organization to arise. In the ZFEL model, dynamic nodes represent entity variation. When compared to the random model, which lacks
such variation, the ZFEL model illustrates two valuable points. The first is about group isolation and the importance of novelty, and the second is about group integration and the importance of selection.

### 2.4.1 Novelty in Group Formation

There is a small tendency for groups to emerge in a completely random environment; however, the window for such emergence is very small (see Figures 14-18). One virtue of the ZFEL model is that when differentiated nodes are in the minority, they act like hubs, i.e. nodes with many edges. This is because when only a few nodes have varied, the remaining unvaried nodes cannot form edges with each other (they can only connect with a differentiated node). This restricts where edges can form and makes it more likely that edges will form a cluster, cycle, or even a clique, if the number of differentiated nodes is small enough. This hub-like behavior among few differentiated nodes can be likened to an innovative or novel difference, which often increases the number of possible new and exploitable connection types. Consider the three examples from section 2.1, the evolution of sex, the evolution of multicellularity and the evolution of coloniality. In a group of homogeneous entities, if a small number of those entities vary in innovative ways, then, as discussed above, a group of sexual-type organisms, adhesive-type cells, or specialized-type insects, can form in isolation from the rest of the asexual, non-adhesive, or non-specialized, entities, respectively. In an entire network of entities, the heterogeneous ones are more likely to form isolated groups.
2.4.2 Selection and Group Stability

The ZFEL model provides a how-possibly explanation for the emergence of groups assuming only variation and random interaction. This is a strong argument against the generally accepted assumption that groups are a product of selective forces; however, the ZFEL model also illustrates that selection is a necessary component for group stability. Unlike the random model, edges in the ZFEL model do not necessarily persist for more than one generation. This is because edges are lost when one of the nodes that formed that edge changes states. This slows down the rate of edge accumulation and creates longer periods of time when the network is only moderately connected and groups form more easily (see Figures 14 and 15). The fact that edges can be lost also means that those groups that form are rather fleeting and unstable, and need an evolutionary force or constraint to stabilize them (such as natural selection).

Returning to the example of complex insect societies, Beshers and Fewell say, “Although selection undoubtedly shapes social organization, it acts on a social unit that already has intrinsic properties. Some of the fundamental properties of social organization, including division of labor, are likely present at the origins of sociality. They are not necessarily produced via selection, though they may be subsequently molded by selection” (2001, p. 434, my emphasis). The ZFEL model demonstrates how a property like division of labor can arise initially such that selection can then refine and perfect it.
Although this project did not study the stability of groups, future work could certainly examine the persistence of groups in the ZFEL model and in a ZFEL model modified with evolutionary forces and constraints that help maintain those groups. A possible way to study this would be to focus on group integration. In this chapter, cliques represent the subgraph with the most integration or interconnectedness among nodes. Clusters may be isolated groups within a network of nodes, but the interrelatedness of nodes in a cluster is weak. A cluster is like a raw and imprecise group representing, for example, the beginnings of division of labor or the very beginnings of adhesivity. A clique on the other hand, which very rarely emerges spontaneously (see Figure 13, and Figures 34 and 35 in Appendix A), is like a refined group, and would be more likely to emerge and persist with the help of evolutionary forces and constraints.

One method in network theory for studying different types of groups focuses on edges, incorporating weighted edges or different edge strengths among nodes (Albert and Barabási 2002, pp. 92-3; Newman 2003, pp. 171-2, especially fig. 1.4). Although this method could be useful, an alternative would be to focus on different node dynamics. The ZFEL model could be modified to include the assumption that individual node

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7 A great amount of integration and interconnectedness among nodes is also known as high modularity in network theory. Although the definition of modularity varies in biology, the use of the term in network theory is consistent with an operational definition of modularity sometimes used in biology (See (See Dassow and Munro 1999, p. 312)).
change is contingent on what group-type connections those nodes have already formed. There would no longer be a single probability of change applied to all nodes. Instead, those nodes that are part of highly integrated groups, such as cliques, would have a severely decreased probability of changing, and the group would be more likely to persist (although there would still be the probability that it would disappear). Nodes in clusters would be less likely to change than ungrouped nodes, but more likely to change than nodes in cycles or cliques. Less integrated groups are “molded” into more integrated groups. Thus, one way to investigate how forces and constraints can alter group stability and persistence within the ZFEL model framework would be to focus on the dynamics of nodes and edges in relation to the type of group they compose.

2.4.3 Group Formation and Biological Hierarchy

To understand the origins of biological hierarchy and the evolutionary transitions, one must first understand the formation of groups. Typical investigations focus on adaptive contexts and search for selective explanations. As Samir Okasha says, “It is also clear that a Darwinian approach to the transitions is essential—we need to understand the selective forces at work, not just the mechanistic details of how the coalescing happened. For example, to understand the origin of the eukaryotic cell, we need to know why, not just how, ancient prokaryotic cells came to contain organelles, i.e. what were the adaptive advantages, and for whom” (Okasha 2007, p. 225). The ZFEL model, on the other hand, presents an environment without any forces or
constraints, and shows how groups can emerge at any level of biological hierarchy. It is an illustration of the mechanistic view that groups can form at any level of organization when there is variation among entities. Selective forces or adaptive advantages are unnecessary for group formation, and in fact, seeking such causes can be misleading.

The Zero Force Evolutionary Law has implications for how to discuss biological hierarchy as well as how to approach questions about the emergence of hierarchical levels. Specifically, it has significance for the question of why entities, capable of independent replication, would forgo that advantage to replicate only as part of a group, which is the topic of the next chapter.
3. The Origin of New Levels of Hierarchy and Why Selection is Not the Answer

In perhaps the most well-known text on the evolutionary transitions, Maynard-Smith and Szathmáry claim “One feature is common to many of the transitions: entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it” (1995, p. 8). The question that naturally follows, is, “Why did not natural selection, acting on entities at the lower level (replicating molecules, free-living prokaryotes, asexual protists, single cells, individual organisms), disrupt integration at the higher level (chromosomes, eukaryotic cells, sexual species, multicellular organisms, societies)?” (1995, p. 8).

Answers to this question often show that being part of the “whole” is more advantageous than being solitary. However, though this may answer the question of how group structure is maintained, I argue it does not, and cannot, answer the question of how a group was formed initially from independent organisms. Clearly, there are two distinct questions: 1) how a new level of hierarchy is maintained, and 2) how a new level of hierarchy arises. I argue that most extant explanations for the second question usually fall into the realm of the first. This is because of the selective framework that is deemed necessary for biological hierarchy discussions, which implicitly shifts the focus from initial group formation to group adaptiveness and maintenance. Besides ignoring the fact that these questions are distinct, appealing to group advantages to explain group
origin is logically incoherent because it presupposes the existence of the very entity that is being questioned!

To keep the issue of origin distinct, as well as approach it correctly, I provide an explanation for group and level origin that does not presuppose the Darwinian framework. Instead of searching for the adaptive advantages that led to group formation, I assume, under the framework of the Zero Force Evolutionary Law (ZFEL), that when selection is weak or absent, groups and new hierarchical levels emerge “for free.” The ZFEL states there is an ever-present tendency for an evolutionary system to increase in variance, and it is this tendency that I argue produces groups and new levels of hierarchy.

I begin by briefly discussing the evolutionary transitions literature and the Zero Force Evolutionary Law. I then demonstrate how assuming a condition of increasing variation results in groups as well as new hierarchical levels. Finally, I present some empirical examples to further justify my general theory about the evolutionary transitions.

3.1 Adaptive, For Whom?

In biology and in philosophy of biology, ‘evolutionary explanation’ and ‘selectionist explanation’ are virtually synonymous. As the quotes below show, this is particularly true of the evolutionary transitions literature. Thus, when discussing the
evolutionary origins of a new level of hierarchy, the result is usually a question about selective advantages:

It is also clear that a Darwinian approach to the transitions is essential—*we need to understand the selective forces at work*, not just the mechanistic details of how the coalescing happened. (For example, to understand the origin of the eukaryotic cell, we need to know why, not just how, ancient prokaryotic cells came to contain organelle, i.e. *what were the adaptive advantages*, and for whom.) (Okasha 2006, p. 225, emphasis added)

The fact that there has been a frequent repetition of the evolution of multicellularity forces us to ask the question, *what could have been the selective pressure* that might have brought this about? (Bonner 1998, p. 65, emphasis added)

In contrast to rare (or even singular) evolutionary transitions, the developmental and evolutionary lability of the transition to multicellularity permits analysis of both *the selective forces favoring the evolution of a major transition* and the adaptive mechanisms that control defectors and stabilize the transition. (Grosberg and Strathmann 2007, p. 624, emphasis added)

*The transitions must be explained in terms of immediate selective advantage* to individual replicators: we are committed to the gene-centered approach outlined by Williams, and made still more explicit by Dawkins. (Maynard Smith and Szathmary 1995, p. 8, emphasis added)

Despite the obvious importance that natural selection plays in biological research and explanation, I argue that for this debate, assuming it to be a necessary feature leads to an explanatory dead end. The authors quoted above all make two assumptions: a) To explain an evolutionary transition is to show how selection favors the transition; and b) Such explanations face a problem, namely that what is good for the new higher level need not be, and usually is not, good for the old lower level. This is the problem of conflict of interests between adjacent levels of biological organization. For instance,
what is good for the single free-living cell is different from what is good for a multicellular collective. Or, to give an example more familiar to philosophers, as is obvious in the case of altruism, what is good for the individual organism need not be what is good for the group.

The conflict-of-interest problem is real, but to even address it, one who attempts to explain evolutionary transitions in purely selectionist terms faces an insurmountable problem. Selection at the level of multicellular organisms may favor multicellularity, but such selection presupposes the existence of multicellular groups. How do these groups arise? Not by selection at the cellular level since that will typically oppose giving up reproductive potential. Nor will selection at the multicellular level work, because, by hypothesis, no multicellular groups yet exist. Thus, the pure selectionist is faced with a paradox: either the higher level entity exists prior to selection at that level, in which case selection does not explain its origin; or the higher level entity does not yet exist, in which case selection cannot lead to it. Of course, this paradox is easily resolved by simply removing the assumption that all evolutionary explanations are selectionist explanations.

As I mentioned earlier, there are two distinct questions to ask about hierarchical levels:

1) How is a new level of hierarchy maintained?
2) How does a new level of hierarchy arise?
If we rewrite these questions as the authors of the quotes above might, they become:

1) How are the selective forces at the higher level able to overpower the selective forces at the lower level?
2) How were the selective forces at the higher level able to overpower the selective forces at the lower level?

There is no longer much of a difference between the two questions, and the second question results in a paradox: *how to explain the origin of an entity by appealing to its selective advantages, which depend on the entity’s very existence.* In other words, approaching the question about level origin from an adaptive perspective presupposes that the level already exists such that it has adaptive advantages. The goal of this chapter is to show that one can address the question of how a new hierarchical level might arise without assuming the answer to be selective. And in doing so, this removes the paradox.

### 3.2 The Zero Force Evolutionary Law

In order to step outside the typical selective framework, I appeal to the Zero Force Evolutionary Law (ZFEL). As I explained in the last chapter, generally formulated, the ZFEL says: “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” (McShea and Brandon 2010, p. 4).

“Diversity” is defined the conventional way as “a function of the amount of variation among individuals” and complexity is defined more technically as “a function only of
the amount of differentiation among parts within an individual.” Unlike colloquial usage, complexity in the ZFEL-sense has no functionality attached to it. Diversity and complexity both measure variation among entities, just at different focal levels. Diversity measured at level n is complexity measured at level n+1. That is, an increase in the diversity of cells in an organism is also an increase in the complexity of the entire organism. More generally, diversity is a measure of external-variance and complexity is a measure of internal-variance. The general idea behind the ZFEL is that variance is expected to increase spontaneously over time.

The ZFEL is a probabilistic process, stating that diversity and complexity will increase on average. To illustrate this, recall Figure 7, introduced in chapter 1 (here as Figure 19), which shows a collection of six particles changing position over four time steps. At T₀, all the particles begin at position 0 and have an equal chance of moving either to the left (-1) or to the right (+1) at T₁. If we focus on an individual particle, it is like a random walk or drift, that is, there is no directional tendency. However, if we look at the group of particles, there is still no directional tendency in the mean position, but, there is a directional prediction about variance—it is expected to increase at every time step because every particle is drifting randomly with respect to every other particle. Eventually, this produces a tendency for the variance (diversity or complexity) of the particles to increase. It is tempting to attribute such variance to drift and conclude that the ZFEL is merely a fancy way of illustrating genetic drift; however, this is conflating
cause with phenomenon. There are many possible causes of variation besides genetic
drift, but that is of no concern in this chapter. The ZFEL describes the phenomenon of
increasing variation and should not be conflated with the possible causes of this
variation.

Figure 19: The expected increase in variance over time in an ensemble of six
particles, as stipulated by the Zero Force Evolutionary Law. Figure from McShea and
Brandon (2010, p. 15).

3.3 Groups for Free

In its general form, the Zero Force Evolutionary Law says there is an ever-
present tendency for diversity and complexity to increase; however, it also makes a
claim about the zero force condition, that is, in the absence of evolutionary forces and
constraints acting on diversity or complexity, the expectation is a continual increase in
diversity and complexity (cf. McShea and Brandon 2010, p. 4). In chapter 2 I modeled
this background condition of increasing diversity and complexity to investigate group formation in the zero force context (Fleming 2012). The model (hereafter called the ZFEL model) has two assumptions: 1) given a group of homogeneous entities, the tendency will be for those entities to vary, and 2) an increase in variation among entities will increase the range of possible interactions between those entities. The first assumption—that entities vary—is based directly on the conclusion of the ZFEL, and the second assumption—that this variation increases the number of novel interactions—is derivative of the law. The basic idea behind the second assumption is this: Imagine a group of entities like single-celled organisms that can only behave and interact in a few ways. If some of the organisms begin to vary, they gain new ways of behaving and interacting. Assuming there is random movement between organisms, the probability of novel and useful interactions increases due to the increase in variation. This argument for self-organization is not new, for example, Kauffman spoke of this phenomenon with respect to molecules (1993; 1995).

As I demonstrated in the last chapter, these two assumptions were modeled using network theory. Recall that in a network, entities are represented as nodes and the connections they form as edges (see Figure 20, which was first introduced in chapter 2 as Figure 8). In a typical random network model, edges can form between any two nodes. In the ZFEL model, however, there are two key modifications. First, nodes are dynamic and change state, which represents the first assumption that entities vary over
time. Second, two unchanged nodes can never form an edge, which represents the second assumption that novel interactions arise from increasing variation among nodes. Thus, in the ZFEL model, the probability of edge formation in an entire network is conditional on the amount of node variation.

![Diagram of a network with eight nodes connected by nine edges.](image)

**Figure 20: An example network with eight nodes connected by nine edges. There is also one unconnected node.**

As I showed in chapter 2, when compared against a purely random model, the ZFEL model demonstrates a higher probability of group formation (see section 2.3 and Figures 11-18). In other words, the ZFEL model shows that the emergence of new variation among entities makes group formation easier. Perhaps contrary to intuition, part of the reason that groups arise in the ZFEL model more than in a purely random model is because of the restriction on edge formation. The dynamic character of the ZFEL model means that the rate at which the network becomes overly connected is substantially slower. When nodes vary, they also lose any edges they formed.
previously, so edges do not necessarily persist beyond one generation. The maximum number of edges possible in a 100-node network is 4950. The random model reaches this maximum after 100 generations; however, the ZFEL model does not even reach 1000 edges in this time (see Figure 15 in chapter 2). The ZFEL model trends to a point of high connectedness, but it does so at a much slower rate and plateaus well before maximum connectedness, thereby creating more opportunities for the emergence of groups. However, the fact that edges do not necessarily persist beyond one generation also means that those groups that do form are rather fleeting and unstable, and eventually need an evolutionary force (like natural selection) or constraint to stabilize them if they are to survive. Thus, as I discuss in the next section, if groups are ever to become new levels of hierarchy, selection and constraints must play a role.

3.4 Origin for Free, Stability for a Cost

3.4.1 Group Origin

The ZFEL model demonstrates that groups can emerge in an environment without evolutionary forces, and that these groups are probable because of hub-like behavior and a slow trend toward connectedness. The ZFEL model also gives an analytic justification, or rather, a how-possibly explanation, for the claim that entity variation makes group formation easier, and in an environment where selective forces and constraints are weak or absent, groups are expected. As entities vary and interact randomly, the range of possible interactions among entities increases, leading to an increase in
actual interactions (associations), which eventually leads to the formation of groups (see Figure 21). In other words, the ZFEL model and Figure 21 provide an answer for the second of the two questions I posed at the start—How does a new level of hierarchy arise?

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**Figure 21: An abstract representation of how group formation is expected by the Zero Force Evolutionary Law (ZFEL), based on results from Fleming (2012).**

Take, for example, the origin of multicellularity that I mentioned in chapter 2. It is likely that multicellular forms originated via the aggregation of solitary free-living cells or via cells remaining attached and not separating after mitosis (Bonner 1998). According to Newman and Muller (2000), both of these scenarios can arise by a simple mechanism of adhesion: “Once one or several adhesive mechanisms were in place, other more complex morphological consequences could have inevitably followed, simply by virtue of variations in cell adhesivity brought about by random processes like metabolic noise, and by the way in which the relevant physical laws act on such heterogeneous cell aggregates” (Newman and Muller 2000, p. 307). This example not only touches upon one of the most well known evolutionary transitions —unicellularity to multicellularity—, but also provides a real world example comparable to the ZFEL model. The “nodes” in this case are single-celled organisms that are homogeneous with respect to the property of adhesivity. Because there is “lax regulation of the abundance
of adhesion proteins” (Newman and Muller 2000, p. 307), cells begin to differentiate with regard to the property of adhesivity, which corresponds to node differentiation in the ZFEL model. As cells begin to differ randomly concerning the property of adhesion, new types of associations—e.g., aggregation or non-separation after mitosis—become possible and eventually new types of associations occur. Regarding aggregation, “Cells with different amounts of adhesion molecules on their surfaces, for example, tend to sort out into islands of more cohesive cells within lakes composed of their less cohesive neighbors. Eventually, by random cell movement, the islands coalesce and an interface is established, across which cells will not intermix (cf. Steinberg and Takeichi 1994; Steinberg 1998)” (Newman and Muller 2000). Regarding postdivision adhesion, Ratcliff and colleagues (2012) used gravity to isolate primitive clusters of cells in the unicellular yeast Saccharomyces cerevisiae. Over time, “snowflake-type” clusters were produced “via successive divisions of component cells” (p. 1596). In this experiment, the largest clusters were selected out of the population every 24 hours. To investigate the ZFEL tendency and group formation, the selective component would need to be removed, resulting in an experiment similar to the initial collection of clusters. In this way one could investigate the different varieties of primitive clusters that arise completely by chance in a population of S. cerevisiae based on random variation in postdivision adhesion.
3.4.2 Group Stability

As I mentioned at the end of section 3.3, one consequence of the ZFEL model is that groups are lost as quickly as they are formed when variation is unrestrained. Thus, the primitive group formed in Figure 21, if it is to become a new level of hierarchy, needs selective forces to stabilize it so it can so it persist. Focal level entities will then eventually become parts, creating a new entity, which then becomes the new focal level (see Figure 22). A boundary shift has occurred. First, the primitive group (a result of the ZFEL) becomes more internally integrated and externally isolated. Associations, which can be connections, behaviors, or reactions between entities, range from temporary to more permanent. To become more integrated, associations in a primitive group become stronger and/or greater in number. An increase in integration is also an increase in isolation, assuming the group is separate from the entire population. As a group becomes more “group-like”, it becomes selectable, and if it is advantageous, (most likely) selection will perfect and stabilize it, creating a new level of hierarchy. At this point the boundary shift is complete and the original entities are now parts in a new entity at a new focal level. This new entity reproduces, and assuming some hereditary fidelity, produces many homogeneous copies of itself such that the process of forming a new hierarchical level can begin again. This process is abstractly represented in Figure 22, which illustrates the answer to the first question—How is a new level of hierarchy maintained?
Figure 22: An abstract representation of how a primitive group (resulting from the ZFEL) requires natural selection (NS) to become a stable new level of hierarchy.

Figures 21 and 22 illustrate the distinction between the question of origin and the question of maintenance. The necessary separation of these questions with respect to the evolutionary transitions is deeply tied to the conflict-of-interest problem mentioned earlier. In the example of cell adhesion, presenting a mechanistic, rather than selective, account of origin dissolves the conflict-of-interest problem. The experiment on yeast clusters illustrated that after primitive clusters arose by chance, continued selection on those clusters resulted in multicellular snowflake phenotypes. The rest of the aggregation story, which is another possible way for multicellularity to arise, is something like the following: some islands of more cohesive cells increase in internal integration and form selectable groups that eventually are perfected by selection such that a new stable level of hierarchy (multicellularity) emerges. From the vantage point of the single cell, giving up full reproductive rights to be part of a group is not advantageous, however, once cells are part of a primitive group, there is now the possibility of selection at the level of the multicellular collective that overpowers selection at the level of the individual cell. This selective explanation is only logically coherent assuming a multicellular collective already exists. Thus, when explaining the
evolutionary transition from unicellularity to multicellularity, it is clear that the question of origin, represented in Figure 21, need not appeal to selection, whereas the question of maintenance, represented in Figure 22, does require selection.

As a second example, take the common problem of altruism, specifically, strong altruism, which involves an absolute cost to altruists. The same conflict-of-interest problem arises here as with single cells. To explain the origin of strong altruism, Fletcher and Zwick (2004) present a multigenerational model with parameters for population size and stochasticity, which studies random interactions between organisms that vary with respect to altruism. Their results show that there is some randomly generated positive assortment (altruists pairing with altruists) after the first generation, although being in a group of altruists, initially, provides no benefit over being in a group of non-altruists. However, by the second generation, this positive assortment becomes advantageous enough to be selected, in other words, the primitive group becomes a selectable group. When the variation among individuals is slight, and only a few, probably rather weak, altruists exist, there is little group formation and no selection of altruism. As variation continues and stronger altruists emerge and begin randomly assorting, beneficial altruist-type groups begin to emerge that are possibly advantageous. As Fletcher and Zwick say, “the positive assortment that develops between randomly created multigenerational groups can suffice for between-group selection to dominate within-group selection and thus for strong altruism to evolve” (cf.
p 311). Similar to the case of cell adhesivity, it is only after primitive group formation that higher-level selection can dominate and an appeal to selection is appropriate.

In the next section I make this point even clearer by confronting, in more detail, the example of the evolutionary transition from solitary individuals to colonies with division of labor and non-reproductive castes.

3.5 The Conflict-of-Interest Problem

In investigating the origin of colonies with division of labor and non-reproductive castes, the same problem arises as with multicellular organisms and altruism: how is something that is not initially adaptive, selected? More specifically, why would solitary organisms, fully capable of independent replication, forgo that advantage to replicate only as part of a group? A possible selective explanation is the following: solitary organisms were selected to cooperate and form groups, then those groups with specialized organisms, and eventually groups with division of labor and non-reproductive castes, were selected. However, not only does this explanation fall prey to the conflict-of-interest problem in its very first step, but it is also completely misguided with respect to how we are to understand the origin of division of labor.

3.5.1 Division of Labor

As I mentioned in chapter 2, Beshers and Fewell give an argument very similar to the one I am presenting: “Although selection undoubtedly shapes social organization, it acts on a social unit that already has intrinsic properties. Some of the fundamental
properties of social organization, including division of labor, are likely present at the origins of sociality. They are not necessarily produced via selection, though they may be subsequently molded by selection” (2001, p. 434). Their argument is based primarily on the threshold hypothesis, which states that organisms like social insects vary in their response thresholds or “intrinsic sensitivities” to task stimuli (Page and Mitchell 1991; Page 1997; Fewell and Page 1999; Beshers and Fewell 2001; Jeanson et al. 2005; Nowak et al. 2010). This can also be called the dirty roommate hypothesis, that is, as the trash becomes full enough to take out, the roommate with the lowest tolerance or lowest threshold for messiness will end up taking out the trash and the others will not. This phenomenon is shown quite easily in the solitary carpenter bee, Ceratina flavipes, which, when forced to cohabit, spontaneously produces division of labor (Page 1997). In nature as a solitary individual, each bee has a list of ordered tasks to complete; however, because of different sensitivities, when forced to cohabit, some bees more quickly approach the first task, which in this specific example is boring out the centers of plant stems. As the other bees approach the boring task, finding it filled, they move on to the second task, foraging for pollen and nectar. The next set of bees, which have an even lower threshold, find the first and second tasks occupied, so they in turn move on to the third task. It was in this way that division of labor spontaneously emerged in a group of solitary bees.
According to Page and Fewell (1999), variance in performing behaviors and reacting to external stimuli “is central to task organization, and that task specialization within honey bee colonies self-organizes from intrinsic variation among members in their probabilities of performing different tasks” (p. 538). They go so far as to say that division of labor is “an inescapable emergent property of groups in which there is behavioral variation among individuals” (p. 538). In other words, variation makes group formation easier. As additional evidence for this claim, in a recent paper by Jeanson, Kukuk, and Fewell (2005), female halictine bees, from both solitary and communal species, were compared in their abilities to divide tasks when confined. The communal bees differ from the solitary bees in the fact that they make one common nest, which is easier to guard from predators. If you’re giving an account of division of labor based on selection, the appropriate intuition is that the groups of cooperating bees more easily engage in division of labor than the groups of non-cooperating bees. This intuition is wrong: “division of labour within the associations of solitary bees during early nest construction was actually higher than in communal associations” (2005, p. 1191). The solitary halictine bees were more likely to engage in division of labor in forced cohabitation than cooperating halictine bees because of the heterogeneity and variety of behaviors they exhibited. Jeanson et al. go on to suggest that “the transition from solitary to communal living may involve selection against task partitioning” and that “the cooperative interactions displayed by the communal bees might prevent the
development of a division of labor” (2005, p. 1191). In this example, selection for cooperation appears to inhibit the emergence of division of labor.

### 3.6 Conclusion

The theory I present in this paper challenges the typical view that to explain the origin of new hierarchical levels, an appeal to selection is necessary. Instead, as I have shown, selection can hinder the emergence of new levels of hierarchy. Thus, an appeal to selection is not only unnecessary but also misguided.

As I mentioned earlier, there are two distinct questions to ask about hierarchical levels:

1) How is a new level of hierarchy maintained?
2) How does a new level of hierarchy arise?

Rewritten from the typical adaptive perspective, both questions ask how selective forces at the higher level are/were able to overpower selective forces at the lower level. The first question I have no problem with and agree that asking about selective forces is useful and correct; however, the second question, I argue, should be rewritten like this:

2) How did entities at the lower level bring about the initial stages of a higher level making selective forces applicable?

Not only does this distinguish the question of origin from the question of maintenance, but it also removes the conflict-of-interest problem and the resulting paradox about origin: selection at the higher level must dominate selection at the lower level, however, selection at the higher level presupposes the existence of entities at that higher level. A
non-selective approach to the question of origin removes the problem of trying to explain the origin of something using properties that depend on its existence. We can solve the paradox by removing it. I argue that explaining an evolutionary transition does not require showing how selection favors that transition. Instead of asking the adaptational question, “Why were lower level units selected to form a group?” I argue it is better to ask the mechanistic and non-selective question, “How did variable units interact and create a group worth selecting?”

More generally, I present the challenge of stepping outside the natural selection framework in all fields of evolutionary study, with a reminder that an evolutionary explanation need not be a selective explanation. Despite the clear importance and occurrence of natural selection, there is importance too in asking, “what if natural selection is not assumed to be a necessary part of my research, what new questions and perspectives can I now advance?” The final chapter presents some formal work that makes asking this question easier.
4. Quantifying the Zero Force Evolutionary Law

The applications of the Price equation range evolutionary studies, including multi-level selection (Arnold and Fristrup 1982; Damuth and Heisler 1988; Michod 1997; Michod 1999; Okasha 2006; Simpson 2010), cultural and social evolution (Frank 1997; Frank 1998; Henrich 2004), evolutionary epidemiology (Day and Gandon 2006), biodiversity and ecosystem research (Kerr and Godfrey-Smith 2002; Fox 2006; Fox and Harpole 2008; Kerr and Godfrey-Smith 2009; Fox and Kerr 2011), investigations of stochasticity in evolution (Altenberg 1995; Grafen 2000; Grafen 2002; Rice 2004; Rice 2008; Rice and Papadopoulos 2009; Rice et al. 2011) and even language evolution (Clark 2010). Generally speaking, this mathematical truth presented by George Price (1970; 1972) measures the change in the average value of a character in a biological population over time. One virtue of the Price equation is its general applicability to many different types of populations, giving it the flexibility to be relevant to a number of different modern day research areas in evolutionary biology.

In this chapter, I use the Price equation to investigate the Zero Force Evolutionary Law (ZFEL). As I have already mentioned in the past three chapters, the ZFEL, in its general form, is an expression of the underlying tendency for variation to increase over time, among all entities, at all levels of biological hierarchy (McShea and Brandon 2010). It applies to biological populations, such as genes, cells, organisms, and colonies, as well as the underlying physical populations, such as atoms and molecules.
This tendency for variation to increase, stipulated by the ZFEL, aids in spontaneous group formation (see chapter 2 and Fleming 2012) and the emergence of new levels of biological hierarchy (see chapter 3). It has implications for all evolutionary research from neutral mutation theory to theories of diversity and complexity increase over the history of life.¹

At its core, the ZFEL is a statement of probability. Given a system with variation and heredity, absent of selective forces and constraints acting on variance, accidents will accumulate and variation among entities will increase. The ZFEL, in its special form, makes a claim about the zero-force context. For example, imagine a group of six identical asexual entities. Over time, assuming there are no selective forces and constraints acting on the group of these entities (that is, there is no stabilizing selection, selection for divergence, or common developing constraints, for example), each entity (or perhaps “lineage” is more appropriate here) will vary randomly with respect to all other entities. Each varying entity is a mutually independent event, thus, the expectation is that the variance among all entities increases over time (and lineages become more and more distinct). Recall the simple model introduced in Figure 7 of chapter one (here as Figure 23), which presents a simple illustration of this probabilistic idea grounding the ZFEL.

¹ With respect to a) neutral mutation theory, see McShea and Brandon (2010, p. 96), b) the theory of diversity increase over the history of life, see chapter three of McShea and Brandon (2010), and c) the theory of complexity increase over the history of life, see Fleming and McShea (Submitted).
McShea and Brandon present the ZFEL as a theoretical law and do not provide a mathematical formulation of it. Though I understand their motivations for doing so, I also agree with Okasha that “Such a formulation is essential if we are to investigate and integrate the law with other theories of evolutionary dynamics” (2010, p. 318). Hence, in this chapter I present the first mathematical representation of the ZFEL, which is the result of collaboration with Timothy Schwuchow.² We chose to use the Price equation framework because of its establishment in the biological community as well as its applicability to various populations, both biological and physical. I would like to note that although the rest of this chapter is written in first person to stay consistent with the entire dissertation, the mathematical work is collaborative.

In this chapter, I derive an expression for changes in phenotypic variance over time using a simple one-dimensional phenotypic transition model based on Price (1970; 1972). I show that if the assumptions stipulated by the ZFEL—a system must have variation and heredity—hold, the result is an increase in variance. In other words, I establish that the ZFEL is inherently true in Price’s framework. With this formalization of the ZFEL, I investigate 1) the ZFEL as a background tendency in evolutionary systems, 2) the ZFEL as a strongly driven trend over the history of life, 3) the ZFEL as an emergent phenomenon at every level of hierarchy, and 4) the applicability of the ZFEL

² Timothy Schwuchow is currently a graduate student in the Economics department at Duke University. His research focus is dynamic modeling of economic systems.
outside of biology. I hope that the work presented in this final chapter will incentivize those currently working in evolutionary dynamics to incorporate the ZFEL, as well as provide some necessary groundwork for future research on the ZFEL, which, as I illustrate at the end of this chapter, need not be confined to biological systems.

Figure 23: The expected increase in variance over time in an ensemble of six particles, as stipulated by the Zero Force Evolutionary Law. Figure reproduced from McShea and Brandon (2010, p. 15).

4.1 Quantifying the ZFEL

4.1.1 The Price Equation

The typical formulation of the Price equation considers phenotypic character transmission in relation to fitness as a way to understand evolution by natural selection. The main focus is on the change in the average phenotype in a population from one generation (parents) to the next (offspring). Given a population of N individuals, some phenotypic character, $z_i$, is measured where $z_i$ represents the character of the $i^{th}$
individual and $\bar{z}$ represents the character average of $N$. $N$ can be a parental population ($p$) or the offspring of that parental population ($o$). The characteristics are denoted $z_{pi}$ and $z_{oi}$, respectively.

Because character $z$ is being tracked over time, $\bar{z}_p = \frac{1}{N} \sum_{i=1}^{N} z_{pi}$ denotes the average parental characteristic and $\bar{z}_o = \frac{1}{N} \sum_{i=1}^{N} z_{po}$ the analogous offspring characteristic average. It is the case then that $\Delta \bar{z} = \bar{z}_o - \bar{z}_p$. To relate phenotypic character $z$ to fitness, the absolute fitness of the $i^{th}$ individual, $w_i$, which is defined as $i$’s total number of offspring, is divided by the average fitness (average number of offspring) in the parental population, $\bar{w} = \frac{1}{N} \sum_{i=1}^{N} w_i$, thus, $\frac{w_i}{\bar{w}} = \omega_i$, which represents the relative fitness of the $i^{th}$ offspring. Relative fitness is the ratio of each individual’s phenotype to the mean phenotype and implies that $\frac{1}{N} \sum_{i=1}^{N} \omega_i = 1$. Fitness is understood broadly to include anything that affects the survival of offspring. Besides the typical selective understanding of fitness, this notion also includes constraints. This is because relative fitness applies to an entire phenotype, which not only includes features that are kept stable via selection, but also features that are kept stable because they are constrained. The notion of constraints is broad and somewhat messy, which is why for this chapter,
constraints are understood narrowly as those things that direct change, specifically, those things that direct the change in character $z$ and have an effect on the variance of $z$.

The Price equation also recognizes the possibility that an offspring’s phenotypic character, $z_{oi}$, may be different from its parent’s phenotypic character, $z_{pi}$. This is called transmission bias, which can be the result of many possible processes during reproduction such as mutation, recombination, linkage, regression towards the mean, selection at a lower level, or just “developmental noise”, and it is denoted:

$$\Delta z_i = z_{oi} - z_{pi}.$$  

The Price equation, tracking the change in mean phenotype ($\Delta \bar{z}$) between parents and offspring is typically written:

$$\Delta \bar{z} = Cov(\omega, z) + E[\omega \Delta z_i]$$  

The first term, $Cov(\omega, z)$, measures the degree to which differential selection has an effect on phenotypic character $z$.\(^3\) It is the covariance between relative fitness and

\(^3\)Rice (2004) describes this first term as measuring differential survival and reproduction, including both selection and drift. Understanding the place of drift in the Price equation is a difficult and controversial matter because Price did not explicitly incorporate drift. Rice (2004) says that the first term in the Price equation can be understood as encompassing drift because it is not specified what causes the covariance between fitness and phenotype, so the term “applies equally to drift and selection” (p. 168). He does, however, go on to present a new way of formulating the Price equation to measure genetic drift (p. 181-187). Building on Rice’s work, Okasha (2006) presents a causal decomposition of realized fitness to include the change due to selection as well as the change due to drift (pp. 31-33). Although random drift is related to the ZFEL in that it is one possible reason that variance might increase, the ZFEL is about the larger phenomenon of increasing variance, not about the individual causes. Thus, a discussion of drift, which governs means, is outside the scope of this discussion because my focus is on the larger...
phenotypic character. If covariance is positive, the character trait is associated with higher fitness than average. As Okasha says, “The covariance term is therefore a measure of the extent to which the character $z$ is subject to natural selection” (2006, p. 23). The second term, $E\left[\omega_i \Delta z_i\right]$, is the average character change due to transmission bias, weighted by fitness, and denotes the expectation that offspring will represent their parents with respect to the character $z$ (see Appendix B for the derivation of Equation (1) and see chapter 1 in Okasha (2006) and chapter 6 in Rice (2004) for a more detailed derivation and description of Price’s equation).

### 4.1.2 Characterizing Variance

The special formulation of the ZFEL states that in any system with variation and heredity, in the absence of selective forces and constraints acting on variance, variance will increase over time. To model this, the Price equation first needs to be modified to characterize the change in phenotypic variance instead of the change in phenotypic mean. I should also note that, although the notation is different, the mathematical principles I show in this section are basically the same as Rice’s (2004, p. 174).

---

ZFEL phenomenon that governs variance. For a thorough explanation of the relationship between drift and the ZFEL, see chapter 6 in McShea and Brandon (2010).
The absolute variance of character \( z \) in the parental population is denoted by

\[
\text{Var}(z_p) = \frac{1}{N} \sum_{i=1}^{N} (z_{pi} - \bar{z}_p)^2
\]

and the absolute variance of character \( z \) in the offspring population is denoted by \( \text{Var}(z_o) = \frac{1}{N} \sum_{i=1}^{N} (z_{oi} - \bar{z}_o)^2 \). The survival-adjusted (i.e. population-weighted) variance of the offspring characteristic (assuming parental populations are equally sized)\(^4\) is denoted \( \overline{\text{Var}}(z_o) = \frac{1}{N} \sum_{i=1}^{N} \omega_i (z_{oi} - \bar{z}_o)^2 \), which can be rewritten:

\[
(2) \quad \overline{\text{Var}}(z_o) = E\left[ (\omega_i (z_{pi} + \Delta z_i))^2 \right] - (E[\omega_i (z_{pi} + \Delta z_i)])^2
\]

In its fully expanded form it reads:

\[
\overline{\text{Var}}(z_o) = E[\omega_i^2 z_{pi}^2] + 2E[\omega_i^2 z_{pi} \Delta z_i] + E[\omega_i^2 (\Delta z_i)^2] - (E[\omega_i z_{pi}])^2 - 2E[\omega_i z_{pi}]E[\omega_i \Delta z_i] - (E[\omega_i \Delta z_i])^2
\]

Since \( \Delta \text{Var}(z) = \overline{\text{Var}}(z) - \text{Var}(z) \), Equation (2) can be rewritten in terms of change in variance over time as:

\[
(3) \quad \Delta \text{Var}(z) = \text{Cov}(\omega_i^2, z_{pi}^2) + \text{Var}(\omega_i) E[z_{pi}^2] - \text{Cov}(\omega_i, z_{pi})(E[\omega_i z_{pi}] + E[z_{pi}])
\]

\[+ \text{Var}(\omega_i \Delta z_i) + 2 \text{Cov}(\omega_i z_{pi}, \omega_i \Delta z_i)\]

\(^4\) Without loss of generality, I assume parental populations are equally sized. Generalizing to cases where the size of parent populations differs would require simple modifications; however, because this would add math without adding to intuition, it was assumed that parental populations were equally sized.
Equation (3) expresses the relationship between expected change in phenotypic variance and 1) relative fitness, 2) transmission bias, and 3) parental phenotype (see Appendix B for derivation). All the terms in Equation (3), except the three terms that contain a covariance, are nonnegative. Intuitively, $\text{Cov}(\omega_i^2, z_{pi}^2)$ can be negative if parents with less extreme (more moderate) characteristics have relatively more offspring than more extreme parents, which on average leads to concentration near the mean phenotype and less variation. Likewise, $\text{Cov}(\omega_i z_{pi}, \omega_i \Delta z_i)$ is negative when transmission error tends to push toward the mean parental phenotype, reducing overall transmission. The hardest to grasp is the possibility of $\text{Cov}(\omega_i, z_{pi})(E[\omega_i z_{pi}] + E[z_{pi}])$ as a negative, which is an artifact of delineating phenotype on the real line.

### 4.1.3 ZFEL Assumptions

The ZFEL requires a system with variation and heredity, that is, a system where heritable variation arises (in the Price equation this can be represented by the condition that transmission bias $\neq 0$). This necessary condition of heritable variation can be expressed in the Price framework as variation in the characteristic occurring over time:

1. **Increasing Variance Assumption:** Variance in the characteristic due to chance is a random variable with zero mean and some variance $\sigma_i^2$ that does not depend on $i$. In other words, there is an intrinsic rate of change: $\Delta z_i \sim N(0, \sigma_i^2)$. The variance distribution is expected to increase equally on both ends.
The notion of chance in this assumption can be understood as an “internal tendency, in the sense that it is the result of the internal redundancy of biological systems and their consequent tendency to differentiate when variation arises” (McShea and Brandon 2010, p. 127).

The special formulation of the ZFEL (the zero-force condition) requires the further condition that selective forces and constraints affecting variance are absent. This is expressed in the Price framework as fitness (selective forces and constraints) having no effect on parental characteristics or on the intrinsic rate of change established in the first assumption:

2. No Selection or Constraints Assumption: Relative fitness, random noise and parental phenotype are mutually independent, such that their joint distribution can be decomposed: 

\[ f(\omega_i, \Delta z_{pi}, z_{pi}) = f_w(\omega_i) f_\Delta(\Delta z_i) f_p(z_{pi}). \]

This also makes explicit the notion of random with respect to, which grounds the ZFEL, because this assumption applies to each \( i \) individually. Thus, the individual intrinsic rate of change is mutually independent among all \( i \)'s in \( N \).

The second ZFEL assumption can also be broken down such that the independence of random noise and parental phenotype is stated separately from the independence of relative fitness and parental phenotype. This distinction can be used to compare a system that completely lacks selection and constraints, to a system that contains selection and constraints, which have no effect on variance (see Appendix C for details).
4.1.4 The ZFEL Formulation

To express the ZFEL formally, I apply the Increasing Variance Assumption and the No Selection or Constraints Assumption to the Variance equation (3). The first assumption alone has no direct effect on mathematical form; however, with the addition of the second assumption, \( \text{Cov} \left( \omega_i^2, z_{pi}^2 \right) = 0 \), and \( \text{Cov} \left( \omega_i, z_i^2 \right) = 0 \). In other words, when selection and constraints are absent, these fitness terms vanish, and after some manipulation the remaining terms can be rearranged as:

\[
(4) \quad \Delta \text{Var} (z) = \text{Var} (\omega_i) E \left[ \left( z_{pi} + \Delta z_i \right)^2 \right] + \text{Var} (\Delta z_i)
\]

Equation (4) represents the special formulation of the Zero Force Evolutionary Law, i.e. when selection and constraints that affect variance are absent. It characterizes the change in phenotypic variance as the variance in relative fitness times the expectation of the offspring characteristic, plus the variance of the change in the characteristic. The change in phenotypic variation is unambiguously positive since both variance and the mean of a squared random variable are nonnegative. In other words, assuming there is heritable variation that is unaffected by selection and constraints, the expectation is an increase in variance. This result was not built into the Price equation, Variance equation, or two ZFEL assumptions; rather, it was a derived result, illustrating that the ZFEL’s zero-force expectation is inherently true in Price’s framework. Even in the limiting case in which selection and constraints are completely absent from the system (i.e. only the first half of
the second assumption is applied) such that \( \text{Var}(\omega_i) = 0 \), Assumption 1 still guarantees that in expectation, variation is strictly increasing (see Appendix C and the discussion of ZFEL Assumption 2a for details).

Although Equation (4) represents the special formulation of the ZFEL, it also lends itself to the general formulation. It illustrates the accumulation of randomness \((\sigma_A^2 > 0)\), which serves as the background expectation of evolving systems. In the next section I model the ZFEL equation (4) and investigate the ZFEL as a background tendency in evolutionary systems and as a strongly driven trend over the history of life.

4.2 Simulating the ZFEL

4.2.1 The ZFEL as a General Tendency

The general formulation of the ZFEL stipulates that there is an underlying tendency for the variance to increase, though this tendency may be aided or opposed by evolutionary forces and constraints, which affect variance. In simulating Equation (4), I illustrate how a distribution of phenotypic characters changes when selective forces and constraints aid, oppose, and have no effect on, the ZFEL.

To model selective forces and constraints, the second ZFEL assumption is not applied to Equation (3), which preserves \( \text{Cov}(\omega_i^2, z_{pi}^2) \) and \( \text{Cov}(\omega_i, z_i^2) \). A modified ZFEL equation, composed of Equation (3) and ZFEL Assumption 1, was modeled to investigate the relationship between population size and mean change in variance when selective forces and constraints are 1) absent, 2) aiding the ZFEL, and 3) opposing the
ZFEL. A total of 8000 simulations were run for population sizes ranging 1 to 1000 using intervals of 10 in each of the three contexts. The parameters considered were: 1) parental characteristics, generated by normal random variables, 2) an intrinsic rate of change, also generated by a normal random variable, and 3) fitness error, used to generate random differences in fitness. To model a context of selection aiding the ZFEL, extreme fitness values were kept or “selected” whereas when modeling a context of selection opposing the ZFEL, the non-extreme values (close to the mean) were kept.

In Figures 24-26, the dotted black line represents the mean change in variance and the grey area represents the upper and lower bounds of 95% confidence intervals for expected change in variance. Obviously larger populations result in smaller confidence intervals. Confidence intervals are important because the ZFEL is probabilistic, and so decreases in variance are possible. Another factor to take into account is that there is a lower bound of 0 for decreases, whereas there is no upper bound for increases. In Figure 24, selection and constraints are either absent or uncorrelated to the characteristics and thus do not affect variance. This is a representation of the zero-force expectation stipulated by the ZFEL. Figure 25 represents the mean change in variance when selection and constraints aid the ZFEL tendency, and Figure 26 represents the mean change in variance when selection and constraints oppose the ZFEL tendency.
Figure 24: The mean change in variance when selection and constraints are either absent or uncorrelated to variance. The grey area represents the upper and lower bounds of 95% confidence intervals for expected change in variance as it relates to population size.
Figure 25: The mean change in variance when selection and constraints aid an increase in variance. The grey area represents the upper and lower bounds of 95% confidence intervals for expected change in variance as it relates to populations size.
Figure 26: The mean change in variance when selection and constraints oppose an increase in variance. The grey area represents the upper and lower bounds of 95% confidence intervals for expected change in variance as it relates to population size.

4.2.2 The ZFEL as a Strongly Driven Trend

So far in this chapter I have discussed the ZFEL in terms of variance, for ease of calculation; however, as I have mentioned in previous chapters, McShea and Brandon present the ZFEL not in terms of variance but in terms of diversity and complexity. “Diversity” is a measure of external variance (differences among) while “complexity” is a measure of internal variance (differences within); thus, they are the same measurement at different focal levels (see section 4.3.3 for further discussion). The use of diversity in this manner is rather commonplace, however, the use of complexity is operationalized to
be function-free, and is quite different from its colloquial usage. Considered in terms of diversity and complexity, more biological implications of the ZFEL become apparent. For example, although there is a consensus that over the history of life complexity has increased, there is disagreement about the type of trend and underlying mechanism. Specifically, whether the trend is 1) passive (or diffusive), where there is no underlying bias but there is an absorbing boundary so a trend—increase in the mean—is produced, 2) weakly driven, where there is a slight bias, producing a trend where the mean and maximum increase, but not the minimum, or 3) strongly driven, where there is a strong bias, producing a trend where the mean, maximum and minimum increase (see Figure 27).

Figure 27: Strongly driven trend, modified (axes flipped and relabeled) from Figure 5.2 in McShea and Brandon (2010, p. 79).
According to the ZFEL, there is a strong bias for variance increases over decreases.

Hence, the expectation is a trend in complexity increase over the history of life that is strongly driven (assuming no opposing selection or constraints):

The ZFEL predicts that in the absence of selection and constraints— that is, in the special formulation—there is, in every species, a tendency for those parts to become more differentiated over time. Reversals can occur. Parts can by chance become more similar to each other. But mostly they will not. In other words, the special formulation of the ZFEL predicts an increase in complexity in almost every species, in almost every lineage, and therefore a strongly driven trend… (McShea and Brandon 2010, pp. 81-82)

The ZFEL predicts a trend similar to the one in Figure 27 even though, as McShea and Brandon point out, one could interpret the ZFEL as predicting a passive or weak trend. The former makes sense because there is a lower bound (i.e. the simplest organism cannot get any simpler) and the latter makes sense because the ZFEL is probabilistic and one could argue that the bias for increases over decreases is not great enough to produce a strongly driven trend. McShea and Brandon, though, appear assured that the expected pattern is strongly, not weakly, driven: “Interestingly, notice that the ZFEL challenges the standard assumption that a strong drive would be the evidence for selection. Strong selection predicts a strong drive but so does the ZFEL, and the ZFEL does so in the total absence of selection favoring complexity” (McShea and Brandon 2010, p. 82).

To examine this claim and model complexity, I first rewrote the expectation term in the ZFEL equation (4). Since \( \left( z_{pl} + \Delta z_i \right)^2 = z_{oi}^2 \), the expectation term in Equation (4) can be rewritten as: \( \Delta Var(z) = Var(\omega_i) E\left[z_{oi}^2\right] + Var(\Delta z_i) \). In other words, \( \Delta Var \)
becomes larger as $E[z^2_{oi}]$ gets bigger. The term, $E[z^2_{oi}]$, represents complexity in the fact that as $z_{oi}$ gets more different from zero (in the positive or negative direction), the change in variance gets larger resulting in more complex systems, so to speak. It is the expected complexity value across all lineages ($i$). Another way to think about the complexity term, $z_{oi}$, is as representing the distance away from the mean within the spread of expected values. The absolute magnitude of character $z$ can be compared across $i$’s with 0 representing the least complex lower bound. Although I define $z_{oi}$ as a complexity term in this chapter, it is good to note that I am only doing so for the sake of contributing to a specific discussion about complexity and strongly driven trends. I could have easily defined $z_{oi}$ as a diversity term or as a general variance term.

When modeling Equation (4) as a statement about complexity, I incorporate ZFEL Assumptions 1 and 2, which means that over time there is fitness (selection and constraints), however, it is independent of increasing variance (complexity). In other words, there are differences in the number of offspring, but they are random with respect to phenotype. The effect of such independent fitness over time in fact adds noise to the distribution of the population, causing complexity to increase exponentially over time without any aiding selective forces or constraints (see Appendix D for details). An interesting implication of this find is that the ZFEL tendency becomes stronger and more difficult to oppose as variance—i.e. the distribution of a population—increases.
Whereas the complexity over all lineages increases exponentially, the expected complexity within each lineage grows linearly. Figures 28 and 29 plot the complexity of particular lineages ($z_{ol}^2$), specifically, the lineage in each time period whose $z_{ol}^2$, relative to the other lineages, is: 1) in the 95th percentile, 2) the mean, and 3) in the 5th percentile.

Figure 28: The complexity of particular lineages over time. Specifically, the lineage in each time period whose complexity, relative to the other lineages, is: 1) in the 95th percentile, 2) the mean, and 3) in the 5th percentile. Simulation assumes a system with heritable variation and no selective forces or constraints. Complexity scale is linear.

Figure 28 is linear and more comparable to Figure 27, whereas Figure 29 uses a log scale for better comparison between lineages. In Figure 28 it looks as though the 5th percentile “minimum” complexity does not increase, leading to the conclusion that the ZFEL is not a strongly driven trend; however, in Figure 29 it is clear that the 5th percentile is
increasing, though much more slowly relative to the other two lineages. A strongly driven trend requires the actual minimum to be increasing, and although the 5th percentile is increasing, this does not exclude the possibility that the absolute lowest lineage in each time period is 0. Thus, Figure 30 plots the absolute minimum complexity, which, although it comes very close to 0, never returns to the absolute minimum.  

![Graph showing complexity over generations](image)

**Figure 29:** The complexity of particular lineages over time. Specifically, the lineage in each time period whose complexity, relative to the other lineages, is: 1) in the 95th percentile, 2) the mean, and 3) in the 5th percentile. Simulation assumes a system with heritable variation and no selective forces or constraints. Complexity scale is log.

---

5 To smooth out the trend line, points represent the actual minimum averaged with the adjacent neighboring points. This clarity measure did not substantially affect the results.
Figure 30: The complexity of the minimum lineage in each time period over time. Simulation assumes a system with heritable variation and no selective forces or constraints. Complexity scale is linear.

This simulation shows that the ZFEL does in fact result in a strongly driven trend, however, the increase in the minimum is very slow and very minimal compared to the increase in the mean and maximum (Figure 28). This has a number of implications for how we interpret the history of life. First of all, it appears that when interpreting a trend over the history of life, specifically, as strong or weak, the maximum is more informative than the minimum. For instance, if cyanobacteria are one of the simplest organisms and represent minimum complexity over the history of life, perhaps the incredibly small increase in complexity from the earliest fossils to modern day cyanobacteria is more significant than we realize. The fact that cyanobacteria have
changed so little over 3 billion years may be because selective forces and constraints are strong, or perhaps they are very weak, and this change is an illustration of the ZFEL tendency at such a low level of variation. Either way, it appears that fairly weak selective forces and constraints can counter increasing variation at this level and produce a weakly driven trend instead of a strongly driven one. This leads to the more general conclusion that the greater the variance (e.g. diversity or complexity), the stronger selective forces and constraints must be to oppose the ZFEL tendency. This is really rather intuitive. To put it in terms of complexity: *stabilizing something that is simple is easy; stabilizing something that is complex is hard.*

### 4.3 A Hierarchical ZFEL

The Price equation is often expressed hierarchically in a recursive fashion to investigate multiple levels of selection (Hamilton 1975; Arnold and Fristrup 1982; Wade 1985; Frank 1998; Okasha 2006; Simpson 2010). For example, Okasha (2006) presents the Price equation in a hierarchically-modified form to measure the total change in mean particle character based on collective-level selection and particle-level selection, where collective character is the aggregation of particle character (see pp. 62-66 for details). Thus, in these hierarchical expressions, there is one reducible character measure. The ZFEL, on the other hand, applies to all levels of biological hierarchy independently, which means that each level requires its own non-reducible variance measure. One way to incorporate hierarchy into Equation (4) is to apply it independently to different levels.
First to a population of entities at one level by defining the characteristic of those entities at the level (e.g. an individual-level trait in a population of individuals), and then separately to a population of entities at a different level by defining the entity characteristic at that level (e.g. a cellular-level trait in a population of cells). In this way one could track the change in variance in, say, a group of individuals, as well as in a group of cells within one of those individuals. But what if we wanted to track the variance at the cellular-level not just within one population of cells, i.e. within one individual, but in the entire population of individuals, similar to the typical hierarchical expression of Price’s equation? What if we wanted to compare the change in variance at two different levels within the same population?

In the next section I present a hierarchical model with independent character measures (one is not reducible to the other) at two different levels of organization that can be compared population-wide. In other words, I characterize how phenotypic distribution changes over time where phenotype now contains a higher-level and lower-level characteristic. I then examine the ZFEL within this hierarchical framework and discuss the implications of such a model.

4.3.1 The Hierarchical Model

To model the ZFEL hierarchically in such a way that we can compare the variance at different levels, I assume some amount of physical nestedness in the structure of those two levels. I continue to assume a population of $i = 1...N$ lineages,
however, rather than treating phenotype $Z_i$ as a scalar, I now assume that each lineage is characterized by an upper level and a set of $M$ lower level components, which are indexed by $j$. The phenotype of each lineage ($i$) is composed of an upper level characteristic $Z_{i0}$ and a vector of lower level characteristics $Z_{ij}$ for $j = 1, \ldots, M$, such that the entire phenotypic state of lineage $i$ can be represented as a $M+1$ vector $Z_i$:

$$Z_i = \begin{pmatrix}
Z_{i0} \\
Z_{i1} \\
Z_{i2} \\
\vdots \\
Z_{iM}
\end{pmatrix}$$

Note that there need not be a direct link between what is represented by the upper level phenotype $Z_{i0}$ and what is represented by each of the lower level characteristics $Z_{ij}$, $j \geq 1$, although there is an assumption that the upper level is in some way structurally composed of the lower level. For example, $Z_{i0}$ could measure variation in cell types and $Z_{ij}$ could measure variation in cell parts, or $Z_{i0}$ could measure variation in organismal height and $Z_{ij}$ could measure variation in hematocytes. The use of variable $z$ to represent both is done as a matter of notational convenience. Like $Z_i$, the transmission noise term, $\Delta Z_i$, is vectorized as:
\[ \Delta z_i = \begin{pmatrix} \Delta z_{i0} \\ \Delta z_{i1} \\ \Delta z_{i2} \\ \vdots \\ \Delta z_{iM} \end{pmatrix} \]

At the upper level, relative fitness \( \omega_{i0} \) is defined identically to relative fitness \( \omega_i \) as it has been used throughout this chapter. However, representing fitness at the lower level is less straightforward because the focus is on the lower-level characteristic at the lower level \textit{as well as} in relation to the higher level. That being the case, relative fitness at the lower level arises due to differences in success rates both \textit{within} each lineage and \textit{between} different lineages. This is because we are looking at the population-wide distribution of the lower level characteristic. A large increase in variation within one lineage at the lower level will not significantly impact the population-wide measure of the lower-level characteristic unless most lineages increase in variation at the lower level. The appropriate expression for relative fitness at the lower level is:

\[ \omega_{ij} = \frac{w_{ij} w_{i0}}{\frac{1}{N} \sum_{i=1}^{N} w_{i0} \sum_{l=1}^{M} w_{kl}} \]

Denoting average upper level fitness by \( \bar{w}_0 = \frac{1}{N} \sum_{i=1}^{N} w_{i0} \) and average lower level fitness as \( \bar{w}_L = \frac{1}{NM} \sum_{i=1}^{N} \sum_{j=1}^{M} w_{ij} \), we can represent this as \( \omega_{ij} = \omega_{i0} \tilde{\omega}_{ij} \) where \( \tilde{\omega}_{ij} = \frac{w_{ij}}{w_L} \) denotes relative
within (the lower level) fitness. Thus, we have shown that overall fitness for each lower level entity, \((i, j)\) is the product of 1) relative upper level fitness and 2) relative lower level fitness. Relative fitness can thus be vectorized as:

\[
\omega_i = \left( \begin{array}{c}
\omega_{i0} \\
\omega_{i0}\tilde{\omega}_{i1} \\
\omega_{i0}\tilde{\omega}_{i2} \\
\vdots \\
\omega_{i0}\tilde{\omega}_{im}
\end{array} \right)
\]

With this notation in place, the upper levels of both Price’s equation (1) and the Variance equation (3) are mathematically the same as their nonhierarchical versions. At the lower level, the form of the Price and Variance equations is the same as their respective upper levels, however, relative fitness now includes relative upper and lower fitnesses, that is, \(\omega_{i0}\) is replaced with \(\omega_{i0}\tilde{\omega}_{ij}\). Hierarchical versions of the Price equation (1) and the Variance equation (3) are represented below as Equation (5) and (6), respectively:

\[
\begin{align*}
\Delta\overline{z}_0 &= \text{Cov}(\omega_{i0}, z_{p0}) + E[\omega_{i0}\Delta z_{i0}] \\
\Delta\overline{z}_L &= \text{Cov}(\omega_{i0}\tilde{\omega}_{ij}, z_{p0}) + E[\omega_{i0}\tilde{\omega}_{ij}\Delta z_{ij}]
\end{align*}
\]

\[
\begin{align*}
\Delta Var(z_U) &= \text{Cov}(\omega_{i0}^2, z_{p0}^2) + \text{Var}(\omega_{i0})E(z_{p0}^2) - \text{Cov}(\omega_{i0}, z_{p0})(E(\omega_{i0}, z_{p0}) + E(z_{p0})) \\
&\quad + \text{Var}(\omega_{i0}\Delta z_{i0}) + 2\text{Cov}(\omega_{i0}z_{p0}, \omega_{i0}\Delta z_{i0}) \\
\Delta Var(z_L) &= \text{Cov}(\omega_{i0}^2\tilde{\omega}_{ij}^2, z_{p0}^2) + \text{Var}(\omega_{i0}\tilde{\omega}_{ij})E(z_{p0}^2) - \text{Cov}(\omega_{i0}\tilde{\omega}_{ij}, z_{p0})(E(\omega_{i0}\tilde{\omega}_{ij}, z_{p0}) + E(z_{p0})) \\
&\quad + \text{Var}(\omega_{i0}\tilde{\omega}_{ij}\Delta z_{ij}) + 2\text{Cov}(\omega_{i0}\tilde{\omega}_{ij}z_{p0}, \omega_{i0}\tilde{\omega}_{ij}\Delta z_{ij})
\end{align*}
\]
4.3.2 The Hierarchical ZFEL Formulation

Representing the premises of the ZFEL in this hierarchical setting requires some minor modification of the ZFEL assumptions from section 4.1.3. The following addendum to Assumption 1 represents the fact that entities at both hierarchical levels have internal rates of change:

H1. Hierarchical Increasing Variance Assumption Addendum: Each of the elements of the phenotypic transmission noise terms $\Delta z_i$ has nonzero variance.

Assumption 2 is modified such that at each level, there is no selection or constraints:

H2. Hierarchical No Selection or Constraints Assumption Addendum: Upper level relative fitness $\omega_{io}$ and random noise $\Delta z_{io}$ are independent of parental phenotype such that their joint distribution can be decomposed as:

$$f_U(\omega_{io}, \Delta z_{pi0}, z_{pi0}) = f_{\omega U}(\omega_{io}) f_{\Delta U}(\Delta z_{io}) f_{pi U}(z_{pi0})$$

Furthermore, lower level relative fitness $\omega_{ij}$ and random noise $\Delta z_{ij}$ do not depend on $\omega_{io}$ and $\Delta z_{io}$, and are mutually independent of $z_{ij}$ and each other such that their joint distribution can be decomposed as:

$$f_L(\omega_{ij}, \Delta z_{pij}, z_{pij}) = f_{\omega L}(\omega_{ij}) f_{\Delta L}(\Delta z_{ij}) f_{pi L}(z_{pij})$$

Thus, the individual intrinsic rate of change is mutually independent among all $i$'s (at both the upper and lower level) in $N$.

Under these assumptions the upper level of the ZFEL hierarchical equation is analogous to Equation (4) and the lower level is the same except that $\omega_{io}$ is replaced with $\omega_{io} \tilde{\omega}_{ij}$:

$$\Delta Var(z_{U}) = \text{Var}(\omega_{io}) \left[ (z_{pi0} + \Delta z_{io})^2 \right] + \text{Var}(\Delta z_{io})$$

$$\Delta Var(z_{L}) = \text{Var}(\omega_{io} \tilde{\omega}_{ij}) \left[ (z_{pij} + \Delta z_{ij})^2 \right] + \text{Var}(\Delta z_{ij})$$

Like with Equation (4), both the upper and lower levels of Equation (7) are unambiguously positive. Furthermore, from Assumption H2 it immediately follows
that $\text{Cov}(z_0, z_L) = 0$. In other words, this expected variance increase is independent at each level. I also verified through simulation that the covariance of the mean upper level characteristic and the mean lower level characteristic is $<0.001$. In this simulation, the number of lineages (upper level) was 100, and the number of lower level components within each lineage was 100. The mean change in variance, in this simulation, over time at the upper and lower levels is seen in Figure 31.

![Figure 31: The population-wide variance of an upper level characteristic and an independent lower level characteristic over generational time in a context absent of selection and constraints that affect variance.](image)

Simulation of Equation (7) illustrates that in a zero-force context stipulated by the ZFEL assumptions, the lower level is expected to increase at a greater rate than the upper level. This is because the lower level incorporates relative upper level fitness and
relative lower level fitness. When both fitness terms are random (selection and 
constraints affecting variance are absent at both levels), this results in more noise.

Similar to the discussion in section 4.2.2, when a population is more variable, the 
distribution of that population, i.e. the variance of the population, increases. This 
concept is explained in more detail in Appendix D. In sum, as Equation (7) illustrations, 
the ZFEL implies that 1) variance increases in expectation at different hierarchical levels 
and 2) this increase in variance is level-independent.

4.3.3 Diversity and Complexity

As I discussed in section 4.2.2, McShea and Brandon present the ZFEL in terms of 
diversity and complexity. These two measures of variance may differ in focal level, 
however, hierarchically, they are “adjacent vantage points” (McShea and Brandon 2010, 
p. 11). Within one level of hierarchy there is a measure of diversity at focal level n 
(external variance) and complexity at focal level n+1 (internal variance). Although 
Equation (7) requires an upper level characteristic \( z_{i0} \) and a lower level characteristic 
\( z_{ij} \) at two different levels of hierarchy, \( z_{i0} \) can be a measure of diversity, complexity, or 
general variance, independent of \( z_{ij} \), and vice versa. Table 10 makes this point more 
explicit by showing four different possibilities with respect to measuring diversity and 
complexity at two levels of hierarchy. Using the cellular level and the subcellular level 
as an example, the difference between hierarchical levels and focal levels is made clear.
Table 3: The relationship between the upper and lower hierarchical levels in Equation (7) and the notions of diversity and complexity in the ZFEL.

<table>
<thead>
<tr>
<th>Hierarchical Level</th>
<th>Variance Measure</th>
<th>Variance Type</th>
<th>ZFEL Focal Level</th>
<th>Example Measure</th>
<th>Equation (7) Possibilities</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper</td>
<td>Complexity</td>
<td>Internal</td>
<td>n+1</td>
<td>Variance within an organism (e.g. number of cell types)</td>
<td>( z_{i0} ) ( z_{i0} )</td>
</tr>
<tr>
<td>Upper</td>
<td>Diversity</td>
<td>External</td>
<td>n</td>
<td>Variance among cells (e.g. distribution of cell sizes)</td>
<td>( z_{i0} ) ( z_{i0} )</td>
</tr>
<tr>
<td>Lower</td>
<td>Complexity</td>
<td>Internal</td>
<td>n+1</td>
<td>Variance within cells (e.g. number of cell part types)</td>
<td>( z_{ij} ) ( z_{ij} )</td>
</tr>
<tr>
<td>Lower</td>
<td>Diversity</td>
<td>External</td>
<td>n</td>
<td>Variance among cell part types (e.g. distribution of cell part type sizes)</td>
<td>( z_{ij} ) ( z_{ij} )</td>
</tr>
</tbody>
</table>

4.3.4 Emergence and Downward Causation

Formulating the ZFEL hierarchically highlights the following two points: 1) variance is measured relative to each level of hierarchy and 2) variance tends to increase at every level of hierarchy independently. Both claims relate to emergence, although the former is epistemological, while the latter is metaphysical. The first claim can be interpreted as an example of “nominal emergence” because variance measures at different levels are incommensurable and irreducible. Variance is irreducible not only because it is level specific, but also because it is a group-level property. The second point makes a stronger, metaphysical, claim that there is an emergent process at every level of hierarchy. This process can be interpreted two ways based on the two different formulations of the ZFEL:
a) Variance is expected to increase at each level of hierarchy independent of every other level given the absence of evolutionary forces and constraints acting on variance at each level (special formulation)

b) There is a tendency at every level of hierarchy, independent of every other level, for variance to increase, although this tendency may be opposed by evolutionary forces or constraints acting on variance at each level (general formulation)

While the former makes a stronger claim about emergent phenomena, it is ideal, and thus, tells us very little about emergence in nature. The latter, while it applies to natural conditions, may be unsatisfying because it only presents an emergent background tendency that may be opposed. Thus, the metaphysical point the ZFEL makes is not about the ZFEL expectation per se, but rather, the claim that there is an emergent process at every level of hierarchy, which includes the ZFEL tendency and the evolutionary forces and constraints that oppose that tendency. It is not merely the phenomenon of increasing variance at every level that is emergent, but rather, the entire process of variance changing over time.

For example, McShea (2002) found that during the transition to multicellular organisms, cells increased in complexity (internal variance) whereas the parts within those cells decreased in complexity. This illustrates the independence of changes in variance at different levels of hierarchy. While variation may increase at one level, it may decrease at an adjacent level. We can also look at this from the viewpoint of the opposing evolutionary forces and constraints. For example, in selecting for larger wings in *Drosophila*, Jablonski (2007) noticed that although selection is on the phenotype,
changes for larger wing size occur by increases in cell size and by increases in cell number. In this example there are constraints at both the wing and cell levels, and there is strong selective opposition to the ZFEL applied to the wing level (specifically to wing size). The lower cell level of the wing has less selective opposition (though constraints are very strong), thus, variance can increase in terms of cell size. Often this example is used to illustrate wing size as an emergent property upon which selection acts, where the changes at the higher level screen off the changes at the lower level (see Brandon 1990 for a discussion of screening off). The ZFEL offers a gestalt shift. This means when discussing emergence, the emphasis is no longer on the selection of emergent traits at multiple levels; instead, the emphasis is shifted such that the entire process of evolutionary change (measured by variance) at any level of biological hierarchy is emergent. The ZFEL formulation (both special and general) begins as “In any evolutionary system in which there is variation and heredity,” where we can interpret each level of hierarchy as its own independent and emergent evolutionary system, so to speak.

This gestalt shift also has consequences for downward causation, a concept often understood as implied by metaphysical emergence. In Jablonski’s example, for instance, selection on the higher-level emergent property—wing size—can be explained as downwardly causing a change in the lower level—wing cells. However, the ZFEL offers a different way to interpret this. There is already the expectation of change at every
level; however, selective forces and constraints at one level can not only oppose variation increase at that level, but also at the levels below. This is very much in line with the rationale behind Equation (7), and with Campbell (1974), who introduced the term using the notion of constraints: “Where natural selection operates through life and death at a higher level of organization, the laws of the higher-level selective system determine in part the distribution of lower-level events and substances” (Campbell 1974, p. 180). Downward causation is merely the higher level determining the distribution of the lower level through boundary conditions (for more detail on the subject of boundary conditions and downward causation, see Eldredge and Salthe 1984). Emmeche and colleagues (2000) echo this notion in their concept of “medium downward causation,” where “higher level entities are constraining conditions for the emergent activity of lower levels” (p. 25). This explanation of downward causation is apparent in Equation (7) because selection and constraints at the higher and lower levels affect the distribution of the lower level phenotype across the entire population. This is because the lower level is nested in the higher level and thus the higher level constrains and directs the ZFEL tendency at the lower level. Although the ZFEL does not require the concepts of emergence and downward causation, it is nonetheless useful to see how the shift in perspective, prescribed by the ZFEL, reforms the discussion of such notions.
4.4 A Universal ZFEL

Near the end of Biology’s First Law, McShea and Brandon offer a generalized ZFEL (hereafter, G-ZFEL) that applies not just to evolutionary systems, but to all physical systems. The G-ZFEL replaces the evolutionary system conditions—variation and heredity—with general system conditions—persistence, variation, and memory (2010, p. 112). Thus, in a system with persistence, variation, and memory, there is a tendency for variation to increase, though forces and constraints may oppose this tendency. Regarding the G-ZFEL, McShea and Brandon say, “developing and arguing for such a principle is beyond the scope of this book” (2010, p. 112) and suggest the reader look at Herbert Spencer’s First Principles (1863). Although it is a bit outside the scope of this chapter as well, it is still worth investigating the G-ZFEL. Mathematically speaking, it is quite easy to show how a formulation of the G-ZFEL naturally follows from the ZFEL equation (4) or the hierarchical ZFEL equation (7). Only a modification of the notation, and a rewording of the assumptions, is necessary, the math is unchanged. Table 2 compares the biological notation used in the Price, variance and ZFEL equations (1-7) to a generalized notation, appropriate for formulating the G-ZFEL.

The biological notation tracks the change in phenotypic mean or variance in a population of individuals with heritable, fitness-varying, traits; however, the generalized notation tracks the change in the mean or variance of a characteristic in a population of entities with memorable, persistent-varying, traits. The main difference is
that the notion of heredity is now replaced with the notion of memory. In other words, there is some memory or consistency guiding how an entity changes over time.

Measuring the change in variance $\Delta \text{Var}(z)$ in a biological system refers to the change in variance of the phenotypic characteristic $z$ over generational time, usually from parental population to offspring population, whereas in a physical system, it refers to the change in variance of a physical characteristic over a period of time, i.e. from $T$ to $T+1$.

Table 4: Examples of typical Price notation applied to biological systems compared to modified Price notation generalized for all physical systems.

<table>
<thead>
<tr>
<th>Expression</th>
<th>Biological Notation</th>
<th>Generalized Notation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N$</td>
<td>Population Size</td>
<td>Population Size</td>
</tr>
<tr>
<td>$i$</td>
<td>Individuals ($0 &lt; i \leq N$)</td>
<td>Entities ($0 &lt; i \leq N$)</td>
</tr>
<tr>
<td>$Z_i$</td>
<td>The scalar phenotypic characteristic of an individual in lineage $i$</td>
<td>The scalar physical characteristic of an entity $i$ over time</td>
</tr>
<tr>
<td>$Z_{pi}$</td>
<td>The parental characteristic in lineage $i$ (ancestor)</td>
<td>The characteristic in entity $i$ at time $T$</td>
</tr>
<tr>
<td>$Z_{oi}$</td>
<td>The offspring characteristic in lineage $i$ (descendant)</td>
<td>The characteristic in entity $i$ at time $T+1$</td>
</tr>
<tr>
<td>$\overline{Z_p}$</td>
<td>Average Parental Characteristic</td>
<td>Average Characteristic at time $T$</td>
</tr>
<tr>
<td>$\overline{Z_o}$</td>
<td>Average Offspring Characteristic</td>
<td>Average Characteristic at time $T+1$</td>
</tr>
<tr>
<td>$W_i$</td>
<td>Absolute Fitness of the offspring of lineage $i$</td>
<td>Absolute Persistence of entity $i$ at $T+1$</td>
</tr>
<tr>
<td>$\overline{W}$</td>
<td>Average Fitness</td>
<td>Average Persistence</td>
</tr>
<tr>
<td>$\omega_i$</td>
<td>Relative fitness of the offspring of lineage $i$</td>
<td>Relative Persistence of entity $i$ at $T+1$</td>
</tr>
<tr>
<td>$\Delta \text{Var}(z)$</td>
<td>Change in variance of the characteristic over time</td>
<td>Change in variance of the characteristic over time</td>
</tr>
</tbody>
</table>
For example, given a population of atoms, each atom \( i \) has a certain measurable characteristic \( z \), such as a state of excitability or a positional attribute (based on distance from atomic neighbors, say). At time \( T \), a population of atoms may be bonded together and have little variance in \( z \). If we apply the following G-ZFEL assumptions, then after some time has passed, the ZFEL expectation would be an increase in variance among the positions of atoms in this population:

**G1. Generalized Increasing Variance Assumption:** Variance in the characteristic due to chance is a random variable with zero mean and some variance \( \sigma^2 \) that does not depend on \( i \). In other words, there is stochasticity: \( \Delta z_i \sim N\left(0, \sigma^2\right) \).

**G2. Generalized No Forces or Constraints Assumption:** Relative persistence, random noise and initial \( z \) (memory) are mutually independent, such that their joint distribution can be decomposed: \( f\left(\omega_i, \Delta z_{pi}, z_{pi}\right) = f_\omega\left(\omega_i\right)f_\Delta\left(\Delta z_i\right)f_p\left(z_{pi}\right) \). This also makes explicit the notion of random with respect to, which grounds the ZFEL, because this assumption applies to each \( i \) individually. Thus, each entity in \( N \) is independently stochastic.

However, in this hypothetical example, the atoms may not increase in positional variance because of electromagnetic force. This force prevents an isolated atom from persisting very long and the memory, or initial \( z \), of each entity stays relatively stable because those atoms that do not change their position over time are more likely to persist.

It is tempting to compare the generalized ZFEL assumptions to the notion of entropy in the second law of thermodynamics; however, McShea and Brandon do not invoke the second law of thermodynamics for two reasons. First, because they feel they
don’t need to. The ZFEL reduces to probability theory, which is broader than thermodynamics. Second, because entropy is one common measure for everything in physics, that is, “Entropy of the whole is reducible to entropy of the parts” (McShea and Brandon 2010, p. 110). As I discussed in 3.4—The Hierarchical ZFEL—variance measures are level specific, incommensurable, and irreducible. Using the generalized notation and modifying the hierarchy assumptions from section 4.3 with respect to that notation, Equation (7) represents the expectation that variance will increase in physical systems at multiple levels of general hierarchy. In other words, instead of biological hierarchy, in physical systems, hierarchy refers to structural nestedness, such as molecules, which are composed of atoms, which are composed of electrons, and so on. Hierarchy and levels of structural organization are not part of the second law of thermodynamics, but they are part of the G-ZFEL. As McShea and Brandon say, the “ZFEL is, in this way, fundamentally different from the second law of thermodynamics” (2010, p. 111). They advise against the attempt to reduce the ZFEL to physics and instead suggest that the ZFEL be understood as a result of probability theory (2010, p. 12). The G-ZFEL is a general probabilistic claim about systems with variation, memory and persistence, which applies anywhere in the universe, taking hierarchical organization into account; thus, it far exceeds any discussion of an entropy measure.
4.5 Conclusion

Near the end of *Biology’s First Law*, McShea and Brandon discuss the possibility of quantifying the ZFEL: “There would be a formal part based on probability theory. Then we would need two empirical parts” (2010, p. 131). In this chapter I have provided the formal part and laid the groundwork to which two empirical parts may now be added. The first is “empirical data that support the application of the special [zero-force] formulation of the ZFEL” to the particular situation being studied (2010, p. 131). In other words, data about a context where selection and constraints are extremely weak and characters are able to vary randomly with respect to each other. The second is “to empirically measure some intrinsic rate of phenotypic change” in the characters being studied (2010, p. 131). Future research would of course be to fulfill these requests for empirical data, and in conjunction with the formal model, produce “a quantitative model of ZFEL-based change” (2010, p. 131). Decomposing the ZFEL equation (4) into causal factors with the right empirical data would provide great insight into how variance (diversity and complexity) does in fact change in nature. A possible starting point would be data on the variability of nucleotide mutation rates in different regions of the genome. Certain regions such as the coding regions have strong selective forces opposing the ZFEL, whereas other regions such as the untranslated regions, display a rate of internal change closer to the ZFEL zero-force expectation (Park 2009). In theory, empirical data could produce “a quantitative model of ZFEL-based change” based on
the hierarchical ZFEL equation (7), however, the data collection would be much more difficult.

Even without data, the ZFEL formulations in this chapter can be used to investigate many interesting issues in evolutionary biology and philosophy of biology. This chapter has only scratched the surface by investigating the ZFEL tendency in different selective contexts, the ZFEL as a strongly driven trend over the history of life, and the implications of the ZFEL for discussions about emergence, downward causation, and universal biology. Formulating the ZFEL not only allows us to ask new questions about the law itself, but also illustrates the novelty and usefulness of the ZFEL for future evolutionary research. Sean Rice said that “Since the initial work of Darwin and Wallace, it has seemed to many people that at its core evolution has simple and universal principles” (2004, p. 188). Representing the principle of natural selection, the Price equation is often the only mathematical example of such a core evolutionary principle; however, the Zero Force Evolutionary Law is now a second case, just as mathematically simple as Price, but more universal and fundamental.

It could be said that the brilliance of the ZFEL is not in what it says, but what it does. The ZFEL’s claim that variance tends to increase over time is already established in many different forms throughout evolutionary studies. Thus, in a way it is “arranging what we have always known.” The beauty of the ZFEL is its simple
unification of myriad evolutionary theories, presented in such a general way that it can be applied to atoms, ants and asteroids.
Appendix A

This appendix contains the mathematical details of the methods used in chapter two, “Network Theory and the Formation of Groups without Evolutionary Forces”. In the following equations, \( n \) is the total number of nodes. In the ZFEL model, because two undifferentiated nodes cannot form an edge, \( x \) represents the number of differentiated nodes. Similar to cluster calculation (see section 2.2.1), to calculate the probability of a cycle of size 3 (3-cycle) forming in the random model, Eq. A.1 divides the number of possible graphs producing a 3-cycle by the total number of possible graphs that can be formed with \( n \) nodes and three edges. To calculate the same probability in the ZFEL model, Eq. A.2 does the same thing while taking into account the number of nodes that have differentiated, represented by \( x \). To form a cycle in the ZFEL model either all three nodes are differentiated, represented by \( \left( \begin{array}{c} x \\ 3 \end{array} \right) \), or only two of the three nodes must have differentiated. There are three ways to create a cycle with two differentiated nodes. For example, if we look at nodes \( A, B, \) and \( C \) again, with edges \( \{A,B\}, \{B,C\} \) and \( \{A,C\} \), a cycle can have either \( A, B \) or \( C \) undifferentiated as long as the other two are differentiated. This is represented by \( (n-x) \cdot \left( \begin{array}{c} x \\ 2 \end{array} \right) \), which assumes one undifferentiated node and chooses two differentiated nodes to make a cycle. The denominators of both cycle equations were explained in section 2.2.1.
Lastly, to calculate the probability of a clique of size 4 (4-clique) forming in the random model, Eq. A.3 divides the number of possible graphs producing a 4-clique by the total number of possible graphs that can be formed with \( n \) nodes and six edges, and for the ZFEL model, Eq. A.4 does the same thing while taking into account the number of nodes that have differentiated, represented by \( x \). Because all nodes must be differentiated and able to form edges in a clique, for the ZFEL model, the four nodes must be chosen from the number of differentiated nodes, represented by \( \binom{x}{4} \). The denominators of both clique equations were explained in section 2.2.1.
For all of the computations in chapter 2, the value of $n$ was 100, and for the ZFEL model, the following values were input for $x$: 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100. When $x$ is 100 in the ZFEL model, it is equal to the random model, since in both cases all nodes are able to form edges.

As mentioned in section 2.3.2, cycles are more difficult to measure because of the quick shift from few or no cycles emerging (when edge numbers are low) to a somewhat complicated mess of many interconnected cycles (when edge number increase). Part of the problem is, unlike clusters, in graph theory, a node can be in more than one cycle at a time, meaning that when edge numbers increase only by a little, the number of cycles gets extremely difficult for the program to count. This was also a problem with cliques because a node can be in more than one clique at the same time as well. The ZFEL model had a much larger “window” in which cycles could be counted, however, most of those results could not be compared to the random model. Therefore, the most useful data comparing the two models was the longest cycle size over five different edge formation probabilities after ten generations (see Figure 33). There are only two data points to display with the random model (the arrow is the second data point), however, the arrow represents the steep increase expected in the random model based on
individual runs even though the 100 run simulation data could not be calculated. The
trend in longest cycle length in the ZFEL model also increases rapidly, but at a much slower rate.

Figure 32: The longest cycle to form on average in the ZFEL and random network models over five different edge formation probabilities after ten generations in a 100-node network. Cycle length is calculated based on the number of nodes in a cycle. Nodes can be in more than one cycle at a time, meaning cycles can overlap. The reason the random model only has two data points (the arrow is also a data point) is because, after that, the number of cycles was too great for the program to calculate.

The number of simulation runs was 100.
Figure 33: The average size of cliques to form on average in the ZFEL and random network models in relation to the number of cliques to form on average in both models. Clique size is calculated based on the number of nodes in a clique and all simulations were run in a 100-node network. The number of simulation runs was 100, and logarithmic trend lines were added.

The minimum clique size measured was two nodes (an edge), thus, in Figure 34, which shows the average clique size in relation to the number of cliques, it is clear the difficulty of a 3-clique or larger forming in both models, even when the number of cliques is high. This means a 3-clique would likely form in an already very highly connected network. This can bee seen in Figure 35, where the largest clique size is compared to the number of cliques, and gives similar results to Figure 34. Even at very large numbers of cliques, both models still barely produce cliques of size four or five. These numbers are the averages over 100 simulations, however unlike the other data,
because clique size is so variable it is quite possible that with a set of parameters one
simulation run could produce a clique of say, size 6, while the majority of runs only
produce cliques of size 2. It is good to keep this in mind when interpreting the results.
Figures 34 and 35 also have logarithmic trend lines added.

![Graph showing the longest cliques to form on average in the ZFEL and random
network models in relation to the number of cliques to form on average in both models. Clique size is calculated based on the number of nodes in a clique and all
simulations were run in a 100-node network. The number of simulations runs was 100
and logarithmic trend lines were added.]

Figure 34: The longest cliques to form on average in the ZFEL and random
network models in relation to the number of cliques to form on average in both models. Clique size is calculated based on the number of nodes in a clique and all
simulations were run in a 100-node network. The number of simulations runs was 100
and logarithmic trend lines were added.
Appendix B

This appendix contains the derivations to accompany chapter four, “Quantifying the Zero Force Evolutionary Law”.

Deriving Price’s Equation

Mean phenotype among parents, denoted by $\overline{z}_p$, is simply the arithmetic average of $z_{pi}$ over lineages:

$$\overline{z}_p = \frac{1}{N} \sum_{i=1}^{N} z_{pi}$$

Likewise, mean phenotype among offspring (weighted for fitness), which I denote as $\overline{z}_o$, can be derived as follows

$$\overline{z}_o = \frac{1}{N} \sum_{i=1}^{N} \omega_i z_{oi} = \frac{1}{N} \sum_{i=1}^{N} \omega_i (z_{pi} + \Delta z_i)$$

The transition bias equation, $z_{oi} = z_{pi} + \Delta z_i$, is substituted into the first line to produce the second. Given this, the expected change in the mean phenotype of the population, which I denote $\Delta \overline{z}$, can be derived as

$$\Delta \overline{z} = \overline{z}_o - \overline{z}_p = \frac{1}{N} \sum_{i=1}^{N} \omega_i (z_{pi} + \Delta z_i) - \frac{1}{N} \sum_{i=1}^{N} z_{pi}$$
\[ \frac{1}{N} \sum_{i=1}^{N} (\omega_i - 1) z_{pi} + \frac{1}{N} \sum_{i=1}^{N} \omega_i \Delta z_i \]

\[ = \text{Cov}(\omega, z_{pi}) + E[\omega_i \Delta z_i] \]

The last line, which follows from the law of large numbers, is Price’s equation.

**Deriving the Variance Equation**

\[ \Delta \text{Var}(z) = \text{Var}(\omega, z_{wi}) - \text{Var}(z_{pi}) \]

\[ = \text{Var}(\omega_i (z_{wi} + \Delta z_i)) - \text{Var}(z_{pi}) \]

\[ = \text{Var}(\omega_i z_{pi}) + \text{Var}(\omega_i \Delta z_i) + 2 \text{Cov}(\omega_i z_{pi}, \omega_i \Delta z_i) - \text{Var}(z_{pi}) \]

\[ = \text{Cov}(\omega_i^2, z_{pi}^2) + \text{Var}(\omega_i) E(z_{pi}^2) - \text{Cov}(\omega_i, z_{pi}) (E(\omega_i z_{pi}) + E(z_{pi})) + \text{Var}(\omega_i \Delta z_i) + 2 \text{Cov}(\omega_i z_{pi}, \omega_i \Delta z_i) \]
Appendix C

This appendix contains the details of the ZFEL assumptions used in chapter four, “Quantifying the Zero Force Evolutionary Law”.

**Deconstructing the Second ZFEL Assumption**

The first ZFEL assumption, which applies to both the special and general formulations, is the condition that heritable variation arise: $\Delta z_i \sim N(0, \sigma_i^2)$. The second ZFEL assumption, which applies only to the special (zero-force) formulation, is the condition that selective forces and constraints affecting variance are absent. In other words, selection and constraints, represented together as fitness, and the intrinsic rate of change from the first assumption are independent of parental phenotype: $f(\omega_i, \Delta z_{pi}, z_{pi}) = f_{\omega}(\omega_i) f_{\Delta z}(\Delta z_i) f_{z_p}(z_{pi})$. When deconstructed, this second assumption involved two parts:

2a. Complete Absence Assumption: $\Delta z_i$, the random noise due to the first ZFEL Assumption, is independent of fitness or parental characteristics. Formally, for any two functions $f(x)$ and $g(x)$,

$$E[f(\Delta z_i) \cdot g(z_{pi})] = E[f(\Delta z_i)] \cdot E[g(z_{pi})]$$
$$E[f(\Delta z_i) \cdot g(\omega_i)] = E[f(\Delta z_i)] \cdot E[g(\omega_i)]$$
2b. No Opposition Assumption: Relative fitness, $\omega$, is independent of parental characteristics $z_{pi}$ (i.e. relative fitness does not affect the relative size of $i$). Formally, for any two functions $f(x)$ and $g(x)$,

$$E\left[f(z_{pi}) \cdot g(\omega_i)\right] = E\left[f(z_{pi})\right] \cdot E\left[g(\omega_i)\right]$$

Assumption 2a completely ignores selection and constraints and does not take them into account, where as Assumption 2b (combined with 2a) has a notion of selection and constraints built in, however, those selective forces and constraints that affect variance are absent.

For example, applying only ZFEL Assumption 1 and 2a to the Variance Equation, the absolute offspring characteristic variance is strictly larger than the parental characteristic variance, that is, $\text{Var}(z_{oi}) > \text{Var}(z_{pi})$. By definition, $\text{Var}(z_{pi}) = E\left[z_{pi}^2\right] - \overline{z}_{pi}^2$, and the equivalent expression for absolute offspring variation (ignoring fitness) is given by

$$\text{Var}(z_{oi}) = E\left[z_{oi}^2\right] - \overline{z}_{oi}^2 = E\left[(z_{pi} + \Delta z_{i})^2\right] - (E[z_{pi} + \Delta z_{i}])^2$$

$$= E\left[z_{pi}^2\right] + 2E[z_{pi}\Delta z_{i}] + E\left[(\Delta z_{i})^2\right] - (E[z_{pi}] + E[\Delta z_{i}])^2$$

By ZFEL Assumptions 1 and 2a,

$$E[z_{pi}\Delta z_{i}] = 0$$
\[ E[Δz_i] = 0 \]
\[ E[Δz_i]^2 = \sigma_Δ^2 \]

Thus,
\[
\text{Var}(z_{oi}) = E[z_{pi}^2] - E[z_{pi}^2] + \sigma_Δ^2 \\
= E[z_{pi}^2] - \bar{z}_{pi}^2 + \sigma_Δ^2 \\
= \text{Var}(z_{pi}) + \sigma_Δ^2 \\
> \text{Var}(z_{pi})
\]

In other words, the expectation is that variance will increase over time, prior to any consideration of evolutionary forces or constraints (that is, without fitness term \( \omega \)).

**Price’s Equation and the ZFEL Assumptions**

Given Price’s equation above and ZFEL Assumption 2a:

\[ E[ω_iΔz_i] + E[ω_i]E[Δz_i] \] . By ZFEL Assumption 1, \( E[Δz_i] = 0 \), such that

\[
\Delta \bar{z} = \text{Cov}(ω_i, z_{pi}) + E[ω_i]E[Δz_i] \\
= \text{Cov}(ω_i, z_{pi}) + E[ω_i]E[Δz_i] \\
= \text{Cov}(ω_i, z_{pi}) + E[ω_i] \cdot 0 \\
= \text{Cov}(ω_i, z_{pi})
\]
Finally, by definition: \( \text{Cov}(\omega_i, z_{pi}) = E[\omega_i z_{pi}] - E[\omega_i] E[z_{pi}] \). If ZFEL Assumption 2b is made, \( E[\omega_i z_{pi}] = E[\omega_i] E[z_{pi}] \). Thus, \( \text{Cov}(\omega_i, z_{pi}) = 0 \). Under ZFEL Assumptions 1 and 2a: \( \Delta \bar{z} = \text{Cov}(\omega_i, z_{pi}) \), however, the addition of Assumption 2b is necessary for \( \Delta \bar{z} = 0 \).

In other words, in applying Assumptions 1, 2a, and 2b (or Assumptions 1 and 2) to the Price equation, the result is that the mean change in phenotype is 0, as the ZFEL predicts. Assumption 2b (or just Assumption 2) is necessary because the Price equation already has fitness considerations built into it that must be muted to adequately represent the ZFEL.
Appendix D

This appendix contains the details of simulating Equation (4) and modeling complexity increase in section 4.2.2 of chapter four, “Quantifying the Zero Force Evolutionary Law”. In section 4.2.2, $z_{ui}$ represents a complexity term because the discussion is about complexity change over the history of life; however, $z_{ui}$ is just as easily interpreted as a general variance term, which is how I refer to it in this appendix.

In simulating Equation (4) and incorporating ZFEL Assumptions 1 and 2, Figures 28 and 29 of section 4.2.2 illustrate that within each lineage, variation increases linearly. Plotting one lineage displays the internal rate of change, i.e. the accumulation of transmission errors over time. Figures 36 and 37 plot the mean change in variance in the characteristic over all lineages over generational time in four different contexts. A context with high selection variation means there is more random variation in offspring number per lineage than in a context with low selection variation (this could have also been called high relative fitness variation). In both types of environments this “fitness” or “selection” is random with respect to phenotype because evolutionary forces and constraints are absent. A context with high transmission variation means there is a greater rate of internal change than in the context with low transmission variation. In other words, the transmission bias is greater in the former.
Figure 35: Simulation of ZFEL equation (4), tracking the change in variance over time in four different contexts. When selection variation is high, offspring numbers randomly vary by a larger degree than when selection variation is low. When transmission variation is high, the internal rate of change is higher than when transmission variation is low.

As I discussed in section 4.2.2, the expectation term in Equation (4) can be rewritten as: $\Delta \text{Var}(z) = \text{Var}(\omega_i) E[z_{\omega i}^2] + \text{Var}(\Delta z_i)$, which shows that as $\Delta \text{Var}$ becomes larger as $E[z_{\omega i}^2]$ gets bigger. The latter term represents the expected variance value across all lineages. As $z_{\omega i}$ gets more different from zero (in the positive or negative direction), the expectation term gets larger and thus the change in variance gets larger such that there is exponential growth in variance (see Figure 36). In other words, the fact that there is transmission bias and random fitness (ZFEL Assumptions 1 and 2) adds
noise to the distribution of a population. This effect grows stronger as variance increases such that as the trend continues, the expected variance increases exponentially. To reiterate a point in section 4.2.2, this exponential increase over time implies that the ZFEL tendency becomes stronger and more difficult to oppose as the variance, that is, character $z_{ci}$ distribution, in a population increases. This trend is basically the same in environments with high and low random fitness and in environments with high and low internal rates of change, though the former has a bit more of an effect than the latter (see Figure 37).

![Log scale version of Figure 36 simulating ZFEL equation (4), tracking the change in variance over time in four different contexts.](image)

**Figure 36:** Log scale version of Figure 36 simulating ZFEL equation (4), tracking the change in variance over time in four different contexts.
References


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Biography

Leonore Fleming was born in Lawrence, KS on March 12, 1983. She received her B.A. in Philosophy and Biology (magna cum laude) from Bucknell University in May of 2005, her M.S. in Biology from Duke University in December of 2011, and her Ph.D. in Philosophy from Duke University in May of 2012. Her publications include: