Explanation and the Evolutionary First Law(s)

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Analogies between Newtonian mechanics and evolutionary processes are powerful but not infinitely versatile tools for generating explanations of particular biological phenomena. Their explanatory range is sensitive to a preliminary decision about which processes count as background conditions and which as special forces. Here I argue that the defenders of the zero-force evolutionary law are mistaken in defending their decision as the only appropriate one. The Hardy–Weinberg principle remains a viable option that is consistent with the epistemic role of Newton's own first law, and the strengths and weaknesses of each analogy are sufficiently distinct to justify their continued coexistence.

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1. Introduction. What does it mean to say that a process like natural selection or genetic drift is an evolutionary force? Much recent work on this question has focused on the ontological implications of such Newtonian analogies. Do all the causes of evolution count as forces (e.g., Sober 1984; Stephens 2004; Filler 2009), or only some of them (Brandon 2006; McShea and Brandon 2010a)? Or is the analogical project fundamentally misguided, since the major evolutionary processes are not properly conceived of as causes at all (e.g., Walsh 2000; Matthen and Ariew 2002, 2009; Walsh, Lewens, and Ariew 2002)? Although these are important questions, the Newtonian analogy also demands examination in an epistemic light. To the extent that such analogies are in fact legitimate, in what sense are they explanatory? How do they contribute to the generation of evolutionary explanations, and how do such explanations work?

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In Newtonian mechanics, the first law describes what happens in the absence of applied forces and is therefore fundamental to the generation of particular explanations of physical phenomena. Analogies between physical forces and evolutionary processes date back at least to 1838, when Darwin pictured individuals locked in the struggle for existence as so many wedges forced in upon one another (Stauffer 1975, 631–32). The idea of evolutionary change as the sum of multiple competing forces emerged in the formative years of population genetics and has been commonplace ever since (Dobzhansky 1937; Roughgarden 1979; Hartl 1980; Gillespie 2004; Hamilton 2009).[1] The Hardy–Weinberg (HW) principle has long occupied a fundamental role in the explanation of evolutionary dynamics, and biologists and philosophers alike have often made the additional step of explicitly analogizing it to Newton's first law (Medawar 1960; Ruse 1971; Ayala 1982; Sober 1984).

For philosophers, Sober's careful elaboration of the analogy established the HW principle as the canonical first law for evolutionary theory, but McShea and Brandon (2010) have recently nominated a rival candidate in their zero-force evolutionary law (ZFEL). The nature of this new contender is captured in their title—*Biology's First Law: The Tendency for Diversity and Complexity to Increase in Evolutionary Systems*. The contest between different interpretations of the first law provides a useful opportunity to clarify the structure of explanations based on it and to identify their inherent strengths and limitations.[2]

Biology's First Law has generated a great deal of lively discussion among philosophers both in person (e.g., Brandon 2010b; Erwin 2011; Huang 2011; Turner 2011) and in print (e.g., Barrett et al. 2012; Brandon and McShea 2012). Much of this conversation has centered on the coherence of the ZFEL and its supporting conceptual apparatus, as well as its claim to lawhood. In this paper I will set aside these issues to focus on some more general philosophical implications of the ZFEL. Though McShea and Brandon's revision of the Newtonian analogy is significant in its own right, it ultimately functions merely as the means to a much more ambitious end. The goal of the ZFEL is to fundamentally revise the criteria that determine what kinds

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[1] Given the prevalence of Newtonian analogies in scientific practice, questions about their epistemic role will remain relevant whatever the outcome of the debate between statistical and dynamical approaches to evolutionary theory. See Hitchcock and Velasco (2014) for a valuable clarification of the issues currently at stake in this debate.

[2] Though the ZFEL and the HW principle are not the only first laws articulated in the literature, they exemplify the two basic explanatory strategies proposed so far. Like the ZFEL, the principle of drift (PD) offered in Brandon (2006) describes a state of evolutionary change, while the zero-cause evolutionary law (ZCEL) suggested by Barrett et al. (2012) follows the HW principle in specifying the conditions under which a population will experience stasis.

of evolutionary explanations are required by various categories of biological phenomena.[3] It is therefore ideally suited to facilitate an exploration of the way in which such explanations leverage putative first laws of biology.

In the next section, I develop an epistemic analysis of Newton's first law and apply it to both formulations of the evolutionary first law. In brief, this type of law identifies processes that are intrinsic to a system and that are sufficient but not necessary causes of certain events. In the remainder of the paper, I use this framework to challenge some (but not all) of the advantages that McShea and Brandon claim for their interpretation. If the ZFEL is not in fact obviously superior to the HW principle as a generator of evolutionary explanations, how should we choose between them? I conclude by identifying some productive differences between the two interpretations, which seem to constitute sufficient reason to maintain a modestly pluralist perspective on the identity of evolutionary biology's first law.

2. The Epistemic Function of Zero-Force Laws. A major explanatory challenge in evolutionary biology is to identify the historical processes that produced the patterns we see in the features of living organisms and in the relics of extinct ones. A theory of forces facilitates this task by describing individual evolutionary causes and determining what will happen to a population in which various combinations of these causes are at work (Sober 1984). The resulting models can help identify which processes might have actually produced an observed pattern, in some cases by discriminating among different causal scenarios that might conceivably produce similar patterns.

In developing the Newtonian analogy, Sober begins by recognizing the central place of the first law in the theory of Newtonian mechanics: "Various forces are described, but the theory has at its conceptual center a view of what will happen to the systems it describes when no forces at all impinge" (1984, 14). This central role is primarily an epistemic one: armed with a description of the zero-force state, an observer can identify situations in which a force is at work. "In evolutionary theory as in Newtonian physics, the principal use of a zero-force law is to discover when evolutionary forces *have* played a role" (34).

Historians and philosophers of physics have also identified this epistemic function as an important part of Newton's own intentions for his first law, which he formulated as follows: "Every body perseveres in its state of rest or of moving uniformly straight forward, except insofar as it is compelled to change its state by forces impressed" (Newton 1999, 416). As Torretti

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[3] McShea and Brandon readily admit that their project is an ambitious one, but they also maintain that the ZFEL is an implicit part of the "conventional wisdom" of evolutionary biology (e.g., Brandon and McShea 2012, 737). I discuss this issue further in sec. 8.

(1999) points out, the first clause of the law does not strictly apply to any real object, since the force of gravity acts across all finite distances. Instead, Newton's first law reflects "a *decision* to analyze every *actual* motion into two contributing factors: the present velocity along the tangent to the observed trajectory, and the *change* that it is undergoing" (46). Such analysis facilitates the identification of applied forces; for example, Newton's illustrations of the first law all show how such changes act to generate or maintain curvilinear motion. Consequently, Cohen concludes that "a major purpose of the first law is make explicit the conditions under which we can infer the action of a continuously acting, centrally directed force" (2002, 65).

But the first law does not always provide a definitive explanation of a particular pattern of motion. It tells us only that any body free of applied forces will not change its velocity. From this we can infer that applied forces are at work when any object changes its velocity. However, the first law does not tell us whether there are any other ways to maintain constant velocity. That information is provided by Newton's second law, which tells us that opposing forces of equal magnitude can also maintain an object at constant velocity. In other words, the first law identifies an inherent property of matter, namely, inertia, that is sufficient but not necessary to produce a certain effect, namely, constant velocity, in a physical object. Though it is a useful epistemic tool, the first law is not therefore an all-powerful one: it can only provide unambiguous explanations of those cases in which the specified effect is not present.

Sober explicitly acknowledges this limitation in his presentation of the zero-force law for evolutionary biology, which he identifies with the HW principle of population genetics. For sexually reproducing, diploid organisms, the HW principle describes the relationship between the frequency of alleles in a population and the frequency of the genotypes they constitute (Gillespie 2004). When mating is random, the frequency of each genotype in a new generation is simply given by the product of the frequencies of its component alleles in the parental population.[4] If the population is also free of genetic drift, natural selection, migration, and mutation, allele frequencies will not change from generation to generation, and genotype frequencies will quickly reach equilibrium (Sober 1984).[5]

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[4] Heterozygote genotypes are considered identical regardless of which parent provides which allele. Thus, if the starting frequencies of the two alleles are given by p and q, the frequencies at all future generations will satisfy the following equation, where each term represents the frequency of a particular genotype: $p^2 + 2pq + q^2 = 1$.

[5] The familiar statement that this equilibrium is reached in only one generation is only strictly true of autosomal loci in hermaphroditic species, or in dioecious species in which the allele frequencies are the same in both sexes. If the frequencies differ between the sexes, or if the locus is sex linked, equilibrium takes longer to achieve. See Gillespie (2004) for details.

Recall Sober's claim that "the principle use of a zero-force law is to discover when evolutionary forces *have* played a role" (1984, 34). Such forces can change the frequencies of both alleles and genotypes in the population. When change is observed in either of these frequencies, we know that HW equilibrium has been disturbed and that some evolutionary force must have played a role. As Sober is quick to point out, the zero-force law does not license the reverse inference. If the frequencies remain constant, it may be that no forces are acting, or it may be that multiple forces are acting in such a way as to balance each other's effects. As in the Newtonian case, the source of this explanatory ambiguity is the logical structure of the zero-force law, which describes inherent features of a system that are sufficient but not necessary causes of certain effects. But because evolutionary zero-force laws depend on analogies between biological processes and physical forces, the class of ambiguous phenomena is not fixed but rather depends on the details of those analogies. Consequently, evolutionary zero-force laws and their associated explanatory powers are especially sensitive to decisions about which phenomena are background processes inherent in any biological system and which should be counted as special forces. These decisions provide the material for McShea and Brandon's overhaul of the Newtonian analogy.

3. The Zero-Force Evolutionary Law. McShea and Brandon break up the central claim of *Biology's First Law* into two main parts: "a new law and a gestalt shift" (2010, 7). The new law postulates a universal tendency for diversity and complexity to increase spontaneously in biological entities. McShea and Brandon dub it the "zero-force evolutionary law," or ZFEL.

> **ZFEL.** 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. (4)

This formulation of the ZFEL applies to all evolutionary systems. In those systems that are free of forces and constraints, the ZFEL predicts that "diversity and complexity will increase on average" (3). There has been substantial discussion, both in the original work and in subsequent debates, about what exactly counts as a constraint or force for the ZFEL. For the purposes of this paper, it is enough to note that its background conditions include two processes, drift and mutation, which are singled out as special forces by the HW principle. The reinterpretation of drift is much more radical and has thus been more controversial. Brandon and McShea (2012, 738–40) maintain that mutation can count as a force in some cases, even though it is always part of the background, whereas drift can never be considered a force.

As McShea and Brandon define them, diversity and complexity are mutually constitutive and level-relative concepts that capture variance in biological entities. Diversity characterizes groups of entities, while complexity describes the parts of a single entity; the diversity of individuals in a population or cell types in an organism, for example, can also be described as the complexity of the population or organism. These properties are not tied to any specific measurement and can be quantified using various counting or distance metrics depending on the specific biological application.[6] The increasing variance predicted by the ZFEL can be produced by truly random underlying processes, such as genetic drift in each population of a species, or by processes that are directed but uncorrelated, such as selection on independent traits across the lineages of a clade.

McShea and Brandon's gestalt shift cashes out the epistemic consequences of embracing the ZFEL. Because increases in diversity and complexity are a normal product of the most basic biological processes—heredity and variation—the explanation of such increases does not automatically require the invocation of natural selection, constraints, or other evolutionary causes beyond these background processes. As McShea and Brandon put it, the ZFEL effects "a radical change in our view of what is pattern, and therefore needs special explanation, and what is background" (2010, 5). Their description of this change as radical reflects their reading of "the standard view of evolution," according to which "increases in most variables are understood to require a force, such as natural selection" (6).

To cement the gestalt shift produced by the ZFEL, McShea and Brandon introduce a revised Newtonian analogy. In place of the HW principle, the ZFEL governs the processes in this zero-force state. "We propose that the role the ZFEL plays in evolutionary theory is analogous to inertia in Newton's first law" (6). Just as inertia governs the motion of physical objects free of applied forces, the ZFEL governs the dynamics of populations in the analogous state. There is a twist in the analogy, however. Newton's first law identifies a certain sort of constancy (specifically, constant velocity) as the fate of an object that is free of forces, while the ZFEL identifies a certain sort of change (specifically, an increase in diversity and complexity) as the fate of a biological population that is similarly free. Because of this twist, there is a superficial sense in which the HW principle is more closely analogous to Newton's first law than the ZFEL (Brandon 2010a). Like Newton's first

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[6] In contrast, the HW principle is tied to the metrics of population genetics, which are derived from allele frequencies. I discuss the epistemic consequences of this difference between the two frameworks in sec. 9.

law, it predicts a certain sort of stasis (specifically, in allele and genotype frequencies) as the zero-force state.

A deeper consequence of the disanalogy between the two first laws is that they produce analogous epistemic situations when faced with divergent biological phenomena. A biologist armed with the ZFEL looks to stasis, rather than change, as the sure indicator that an evolutionary force is at work. According to the ZFEL, when diversity and complexity fail to increase over evolutionary time, we can infer that some evolutionary force or constraint is acting to oppose them. When diversity and complexity do increase, however, there are two possibilities. Either there are no forces or constraints acting at all, or they act without negating the background tendency toward increasing variance. In the latter case, the ZFEL tendency may oppose but dominate the forces and constraints, or it may augment their effects.

McShea and Brandon describe the general purpose of a first law in much the same way as I have done here—as a tool for identifying what happens when no forces impinge on a system. They also acknowledge the epistemic limitations produced by the structure of the law. Like Sober, they acknowledge that evolutionary forces can produce the phenomena described by their zero-force law, just as physical forces can produce a state of constant velocity. The rival versions of the evolutionary first law therefore have the same logical structure and exhibit the strengths and weaknesses that it confers. In McShea and Brandon's estimation, however, the HW principle suffers from fatal flaws that should remove it from contention as a zero-force law, while the ZFEL occupies a privileged position of universal appropriateness for evolutionary explanations. In the next section I challenge this argument and show how it loses sight of the shared structural features that I have articulated so far. The additional benefits claimed for the ZFEL are not enough to decide the issue, and it is best to adopt a modestly pluralist perspective on biology's first law.

4. The Case against the Hardy–Weinberg Principle. Why should we embrace the gestalt shift that McShea and Brandon propose? One of the main benefits they promise is an antidote to the strong temptation among both biologists and laypeople to single out evolutionary change as the most pressing explanandum and natural selection as its most likely cause. As they point out, for example, the commonplace that evolution is just change in gene frequencies over time overlooks the importance of stabilizing selection as an evolutionary process. On the other hand, evolutionary trends are often explained by postulating a selective regime that promotes their development. By contrast, the various processes captured by the ZFEL conspire to change biological systems in ways that increase diversity and complexity over time, all without the help of natural selection.

In attempting to correct the privileging of change and selection, McShea and Brandon reserve special ire for the HW principle, which they charge with fomenting serious confusion about the expected outcome of evolutionary processes. Brandon and McShea (2012) give an especially blunt version of their charge: “As a bit of analytic reasoning the Hardy–Weinberg ‘law’ is without fault, but its translation into biology is at best misleading, and, we would say, just false” (742).[7] This is a serious objection that, if true, would immediately disqualify the HW principle from consideration as a zero-force law—as is no doubt the intention.

In this section I show that the charge of falsehood is a red herring. The weight of this claim rests entirely on the premise that drift is not an evolutionary force. All inferences from this central premise are uncontroversial and can be accepted on either interpretation of the evolutionary first law. On the heels of this argument, however, McShea and Brandon raise a question of much more general relevance. To what extent does nature—or at least our empirical interaction with the natural world—determine our choice of a zero-force state? McShea and Brandon present the ZFEL as the only natural and empirically adequate choice for evolutionary biology, leaving the HW principle to stand as a highly misleading substitute. In section 6 I argue that this position rests on a misapprehension of the epistemic function of zero-force laws in general and Newton’s own first law in particular. Once the charges against the HW principle have been cleared, the triumph of the ZFEL will no longer appear to be a foregone conclusion. It can then be appreciated as a powerful epistemic tool that is nevertheless bound by the same kind of structural limitations that restrict the scope of the HW principle. Because the rival first laws run up against these limitations in different real-world scenarios, each has particular strengths and weaknesses that make it more or less suited to certain kinds of explanatory tasks.

To sustain their claim of falsehood, McShea and Brandon need the premise that drift cannot be considered an evolutionary force. This much is implicit in their argument against the HW principle, but what they do not make sufficiently clear is that this premise is in fact the only part of that argument that is in dispute among the various interpreters of the Newto-

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[7] The critique of the HW principle in McShea and Brandon (2010), which closely follows that of Brandon (2006), is more complicated. It introduces two statements of the principle, H-W_1 and H-W_2, and offers two different interpretations of H-W_2. Of the three resulting readings of the HW principle, only one is charged with falsehood, while the others are simply deemed misleading. But as Barrett et al. (2012) point out, H-W_1 and H-W_2 are logically equivalent, and the reply by Brandon and McShea (2012) drops the bifurcation of the principle. Here I respond to a core argument that appears in both publications.

nian analogy. Both statements of their argument suffer from this problem, but McShea and Brandon (2010) further muddy the waters by conflating the concepts of null hypothesis and zero-force law. I address this conceptual problem in the next section, after clarifying the role of the key premise on drift.

Brandon and McShea begin by explaining how the mathematics of the HW principle can be translated to a putative zero-force principle: "One perfectly respectable gloss on the H-W statement is this: If no evolutionary forces (i.e. selection, mutation, migration, non-random mating) act on a population then it will settle into a genic and genotypic equilibrium. . . . That is: If no forces, then no change. That, of course, is logically equivalent to: If change, then some forces have acted. But that, we claim, is not just false, but easily shown to be false" (2012, 742). Here Brandon and McShea offer a very simple paraphrase of the HW principle in Newtonian terms.

$\mathbf{HW_P}$. If no forces, then no change. If change, then some forces have acted.

HW_P would be unobjectionable to any champion of the traditional interpretation and could in fact serve as a summary of Sober's original exegesis. But instead of being a pithy summary of the zero-force law, it is, according to Brandon and McShea, patently false. What makes the difference? Note the parenthetical enumeration of evolutionary forces in the original quotation—"i.e. selection, mutation, migration, non-random mating." The exclusion of drift from this list is of course no accident, and it explains how Brandon and McShea can level the charge of falsehood against an otherwise plausible interpretation of the first law.

Drift is a disruptor of evolutionary stasis and consequently a cause of change in many evolutionary metrics. This much is not in dispute between the two interpretations of the Newtonian analogy. Biologists are not therefore misled when they introduce the HW principle in textbooks, apply it to stable traits in real populations, or use it to build theoretical models of population dynamics. The principle runs into trouble only when drift is allowed into the list of parameters that define a zero-force scenario. If a biological system can be experiencing drift and still count as meeting zero-force conditions, then change should of course be expected and HW_P is obviously false. Conversely, if drift is counted as a force, then it is excluded from the zero-force scenario along with selection and the rest, and HW_P is once again unobjectionable. Either way, there is no disagreement about the relationship between drift and the general phenomena of stasis and change.

So far, it seems that McShea and Brandon's case against the HW principle amounts to nothing more than their exclusion of drift from the list of evolutionary forces. Though they do not say as much, they do at least point the reader toward their published defenses of this position on drift.[8] However, the rest of their argument suggests that there is more at stake than this dispute about drift—instead, the ZFEL view is presented as being in some sense a better match with the observed phenomena of evolutionary biology.

> If one accepts [the exclusion of drift from the list of evolutionary forces], then the issue is what happens when nothing happens (i.e., no forces act). And that is the question a zero-force law is supposed to answer. Our answer is: change happens, more particularly, diffusion happens. The H-W answer is: stasis—i.e., nothing happens. . . . Let us look at a few biological examples to see what light they might shed on this dispute.
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> A gene is duplicated and inserted elsewhere in the genome. Its function is already being performed by the original, so it is freed from selection. What happens? It changes, i.e., it differentiates from the original. A neutral sequence of DNA is fixed in a population that splits, never to come back together. What happens? The two populations diverge in that genetic marker. Two sister species separate. What happens? They diverge in a clock-like manner. Two sister genera continue to persist through time. What happens? They diverge, again in a fairly clock-like manner. The same is true for even higher taxa. (Brandon and McShea 2012, 743)

Like the preceding steps of the argument, there is nothing controversial about these examples. Biologists disagree about the finer points of some of these processes, such as their dynamics and frequency across evolutionary time, but they are all well-accepted mechanisms. A traditionalist interpreter of the Newtonian analogy could happily endorse them as real and important without agreeing that they count as zero-force scenarios. So how do they help Brandon and McShea's case? The closing lines of their argument hint that the processes captured by these examples are not just real and important but in some sense privileged by nature itself. "For now we want to avoid the philosophical dispute about the relation of drift to the other evolutionary factors mentioned in H-W and simply appeal to what the examples above point to. The default condition of evolutionary systems is change, and change of a particular sort—increase of diversity and complexity" (743).

This final claim is the only part of this argument that adds something new beyond the position on drift. By appealing to the "default condition" of evolutionary systems, Brandon and McShea raise a question with much greater epistemic significance than the dispute between rival first laws. What counts

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[8] "Unfortunately for us, the easy showing of this depends on some conceptual brush clearing—which we have done in the book and elsewhere (Brandon 2006), and so will not repeat here. The relevant conceptual distinction is in separating drift (not a vector quantity) from selection, mutation, migration and non-random mating" (Brandon and McShea 2012, 742).

as the default condition of a natural system? How do we recognize it, and what role does empirical observation play? The implicit answer supplied by the biological examples is that change of the sort captured by the ZFEL should be recognized as the default condition of evolutionary systems because it is frequently observed at all levels of biological organization and therefore pervasive in nature. In other words, the ZFEL accurately represents a wide variety of natural phenomena.

Whether or not this claim is true is an empirical question, as McShea and Brandon recognize. However, there is an independent philosophical question as to whether its truth would in fact be decisive for its claim to first-law status. A closer examination of Newton's own first law shows that accurate representation of natural phenomena is not the only way to ground a zero-force law; idealization is also a viable option. Before filling in the details of this argument, however, I will clear up a conceptual confusion that affects the original formulation of McShea and Brandon (2010).

5. Null Hypotheses versus Zero-Force Laws. In *Biology's First Law*, McShea and Brandon often assert the special status of the ZFEL by describing it as the appropriate null hypothesis for evolutionary biology. This description, they suggest, is "an equivalent way of thinking about the zero-force law" and one that "may be more in keeping with most biological practice." The concepts of zero-force law and null hypothesis are equivalent, they explain, "because a null hypothesis just tells you what would happen if nothing special were going on" (McShea and Brandon 2010, 99–100). In its privileging of stasis, they continue, the HW principle "gives exactly the wrong null expectation" (100). Instead of remaining stable from generation to generation, "most populations will change" after a round of reproduction (101).

Here we have essentially the same argument traced in the last section, only couched in the language of null hypotheses rather than default conditions. The appeal to what happens in "most populations" suggests that McShea and Brandon understand empirical accuracy to be a decisive virtue for a putative zero-force law. As in Brandon and McShea (2012), this statement of the argument also closes with an appeal to real-world examples of neutral evolution (McShea and Brandon 2010, 102). Though it does not affect the content of their argument, the terminological difference between these two formulations is important. The concept of a null hypothesis cannot be identified with that of a zero-force law without seriously distorting its ordinary meaning in scientific discourse. Despite some similarities, null hypotheses and zero-force laws should be understood as distinct epistemic tools that serve different explanatory needs.

Null hypotheses facilitate counterfactual reasoning in science. They are typically generated by null models, which describe the activity of a set of causes of interest. In the words of paleontologist David Raup, “Neutral models are useful in testing hypotheses about process. In the typical case, a pattern is seen in empirical data and a mechanism is proposed to explain the pattern. A neutral, or null model is then constructed to answer the question, Would the same pattern have occurred in the absence of the proposed mechanism?” (1987, 121).

When biologists construct null models, they single out certain processes as worthy of special investigation and relegate others to the explanatory background. A zero-force law can therefore be understood as a special kind of null model that specifies what happens when only a few very fundamental background processes are in operation.

The HW and ZFEL pictures disagree about exactly which processes are sufficiently fundamental to count as zero-force conditions and which should be recognized as special causes or forces of evolution. Both interpretations, however, are compatible with the existence of many null hypotheses in evolutionary biology that would not qualify as zero-force scenarios on either analogy. Instead, these hypotheses are generated by null models that incorporate a host of evolutionary processes beyond the scope of either putative first law—for example, a neutral model of trilobite cladogenesis might assume that average rates of speciation and extinction for this group are no different from those of other Paleozoic invertebrates (Raup 1987). Neither the ZFEL nor the HW principle, therefore, should be presented as the one appropriate null hypothesis for evolutionary theory.

6. Default Conditions and Expected Outcomes. The epistemic function of a zero-force law is a special case of a general kind of contrastive reasoning. Rather than defining the effects of a particular process or cause in isolation, we observe what difference it makes to a set of already-specified conditions. A default condition, in this very general sense, can be anything that serves our epistemic purposes by supplying the appropriate contrast to a process of interest. But are there other reasons to grant a privileged status to certain default conditions for a particular natural system? In particular, to what extent should empirical evidence determine the choice?

As rival zero-force laws, the ZFEL and the HW principle take very different positions on this last question. The ZFEL provides an accurate representation of natural phenomena, while the HW principle is an idealization that is only approximately realized in nature. McShea and Brandon imply that only the first strategy is appropriate for a zero-force law, but this is a mistake. Even the paradigm case of Newton’s own first law turns out to be an idealization when properly understood. More generally, however, both strategies have unique epistemic strengths and weaknesses.

When McShea and Brandon set up the analogy between the ZFEL and inertia, their language suggests that nature itself determines the default condition for physical dynamics: “We propose that the role the ZFEL plays in evolutionary theory is analogous to inertia in Newton’s first law. Inertia—lack of change—is the default, or ‘natural,’ state of velocity, the background against which gravity and other special forces act” (2010, 6). I do not want to make too much of this statement, since McShea and Brandon later say that it does not matter to them whether inertial motion is in fact objectively the zero-force state according to our current relativistic physics (149 n. 7). There is, of course, a weak sense in which the zero-force law for physics is natural—the physical concept of force, unlike its biological counterpart, is clearly bounded by a set of well-defined physical processes—though, as Hitchcock and Velasco (2014) point out, these processes are less homogenous than biologists generally recognize. There is one thing that the appeal to nature cannot coherently mean, however. It cannot mean that inertial motion is commonly encountered when we observe the natural world. In other words, it cannot mean what the phrase “default condition” seems to mean when it is applied to the ZFEL.

I have already laid out the reason why this interpretation is untenable in my discussion of Newton’s first law in section 2. Because all physical objects must be a finite distance from other physical objects, there are no objects that are strictly free from the force of gravity. The first law is therefore an idealization that primarily serves to facilitate the analysis of motion and to understand the interaction of inertia with applied forces. Certainly there are some objects (for example, those in deep space) that approximate inertial motion, but they are not the only explananda for which the first law is relevant. There are also many objects that duplicate the phenomena of inertial motion—“persevering in [their] state of rest or of moving uniformly straight forward”—because they are experiencing a balance of forces. But these are not examples of zero-force states. As important as it is, Newton’s first law is not known from empirical examples.

Like Newton’s first law, the HW principle is an idealization that is approximately realized in a few cases but epistemically relevant to many more. While it is true that all real populations are subject to drift, the magnitude of its effect depends heavily on population size. In large populations, the effects of drift are relatively small in comparison to the effects of other evolutionary processes. When selection, migration, and mutation are minimal and mating is random with respect to some allele, HW equilibrium may be approximated by real populations at the locus in question; examples of this phenomenon are standard fare for the introductory chapters of population genetics textbooks (e.g., Gillespie 2004 on placental alkaline phosphatase alleles in an English population; Templeton 2006 on blood types in a Pueblo population). It is therefore common for applications of the law to relax the conditions on its scope to include large populations, not just infinite ones. More importantly, however, the primary epistemic function of the HW principle is not to represent actual populations but to facilitate the analysis of their evolutionary dynamics.

One might object, as McShea and Brandon do, that the HW principle applies only to sexually reproducing organisms and is therefore more of an "accidental generalization" than a law (2010, 102, following Beatty 1981). But as Barrett et al. (2012) point out, laws may be limited in scope without losing their nomological status. More importantly, the HW principle answers for one class of organisms a question that is of general relevance: what is the effect of reproduction alone on the genetic makeup of a population? For the organisms within its scope, the principle yields the significant insight that the Mendelian processes of segregation and independent assortment do not change genotype frequencies at a single locus in the absence of drift, selection, mutation, and other evolutionary forces (Sober 1984). For haploid, asexual organisms outside the scope of the HW principle, it is easier to see that stasis is the zero-force condition.

In nature, of course, even "reproduction alone" is a rather complicated process. Nondisjunction and meiotic drive can distort Mendelian dynamics at individual loci, while linkage alters genotype frequencies and mutation introduces new alleles. Meanwhile, even asexual organisms have evolved mechanisms for the exchange of genetic material. Endorsing a principle like HW need not involve the denial of all this complexity, but can instead provide a solid foundation from which to appreciate it. Hardy's derivation of the principle in fact served just this sort of purpose by clearing up confusion among British biologists about Mendel's principles of inheritance (Edwards 2008), and even Dobzhansky (1937) continued to recognize this simple mathematical formula as the summation of important empirical discoveries.

7. Is Drift an Evolutionary Force? If I am right that McShea and Brandon's charge of falsehood against the HW principle reduces to an assertion of their position on drift, the arguments for that position have the potential to be decisive in the conflict and are therefore worth revisiting. Their claim is that drift cannot be considered a force, and that the HW conditions therefore inappropriately mix forces and non-forces. The main premise of the argument is that evolutionary forces must have a magnitude and direction that can be expressed in some common currency. Because either fixation or loss is always possible for any drifting allele, drift does not have a definite direction and is therefore disqualified as a force. Stephens (2004, 2010) has argued in response that drift does in fact have a specifiable direction—namely, it decreases genetic variation by moving populations toward homozygosity and away from heterozygosity.

Brandon (2006) rejected this criterion and maintained that the ultimate unpredictability of drift makes it inappropriate as an evolutionary force. I think that the ZFEL picture actually strengthens the case for accepting Stephens's suggestion. Whereas Brandon (2006) focused narrowly on genotype frequencies as the common currency for evolutionary change, McShea and Brandon (2010) take a pluralistic and hierarchical approach to tracking the evolution of complexity and diversity. They explicitly claim that the ZFEL should apply to any metric of diversity or complexity at any level of biological organization. This opens the door to population genetic measures of variance, such as heterozygosity, in which drift does create a trend of predictable direction. Even if McShea and Brandon were to insist on sticking to gene or genotype frequencies, however, the direction of drift would not be as thoroughly unpredictable as they make it out to be. If drift is the only evolutionary process at work, the fixation probability of an allele is just equal to its initial frequency in the population. Unless this frequency is exactly one-half, either fixation or loss will be the favored outcome (Filler 2011; Barrett et al. 2012) and is therefore an appropriate choice for the (admittedly probabilistic) direction of drift.

The resolution of this debate ultimately depends on the strictness of the criteria for mapping a Newtonian force to some force-like process in another physical domain. The attainment of definitive and inflexible criteria seems too ambitious a goal for such a complex analogy as this one. As Hitchcock and Velasco (2014) show, even the original Newtonian forces are heterogeneous in their manifestation of several properties that have been taken to be essential for putative evolutionary forces. Filler (2009) makes an attractive suggestion for approaching these analogies: allow evolutionary causes to exist on a continuum of forcehood that distinguishes them according to their mathematical precision and unifying power. Drift, on this view, turns out to be a bit less force-like than natural selection, but significantly more so than many other causes.

There is one final reason that ought to discourage McShea and Brandon's reliance on definitional criteria, namely, that the ZFEL tendency itself seems to satisfy the criteria of forcehood that McShea and Brandon implicitly endorse. It succeeds where drift fails in having a definite direction, namely, toward increasing complexity and diversity. As for magnitude, the increase in diversity and complexity will be stronger or weaker depending on the underlying processes that produce it, and could (at least in principle) be determined empirically with some appropriate metric by choosing situations in which selection and other forces are minimal. The ZFEL further appears to meet some additional basic criteria for biological forcehood proposed by Filler (2009): it is "causally efficacious" in producing evolutionary change (775), and its action depends on the physical properties of biological objects (776).

8. Does the ZFEL Have an Explanatory Advantage? Even though McShea and Brandon's attack on the HW principle does not stand, there are still some positive claims of the ZFEL picture that we must consider. The benefits that McShea and Brandon promise with their gestalt shift emphasize its explanatory power. First of all, the ZFEL aspires to be a law of "universal biology" (McShea and Brandon 2010, 103)—that is, of any system that has heredity and variation. As I argued above, the more restricted scope of the HW principle does not invalidate its claim to lawhood or its explanatory value. However, the greater universality of the ZFEL analogy seems likely to be one of its primary advantages over the HW framework.

Beyond its universality, McShea and Brandon emphasize the ability of their law to provide a common conceptual platform for cases in which ZFEL-like processes are already accepted by evolutionary biologists. At the same time, the principle is supposed to correct what they see as a pervasive misunderstanding, namely, the assumption that evolutionary change (especially increases in diversity and complexity) requires the invocation of special causes (especially selection) and that stasis is therefore the default state of biological populations.

The prospective unification of existing evolutionary explanations is one of the most attractive features of the ZFEL view. There are two primary domains in which McShea and Brandon argue, correctly I think, that something like the ZFEL is already at work. The first is in the field of molecular evolution, where practitioners are used to thinking of mutation as constantly introducing variation into reproducing populations. Some of the most effective models for detecting selection at the molecular level use variation at neutral positions as a baseline against which to assess the variation elsewhere in the genome. The second domain is the explanation of increases in macroevolutionary disparity, or the divergence of phenotypes over long stretches of evolutionary time. Many candidate explanations identify unexplored ecological resources as a key driver of phenotypic divergence. Insofar as different lineages independently develop ways of exploiting such resources, their diversification will fall under the criteria for a ZFEL process. The prospect of uniting processes at such different scales is indeed an exciting one, and its success would be a real advantage for the ZFEL.

The corrective role of the ZFEL also has merit, since McShea and Brandon are right to identify a pervasive tendency to focus on evolutionary change as the most pressing explanandum, and selection as its most likely cause. However, the strength of this preoccupation varies across subfields of evolutionary biology, and McShea and Brandon's own identification of implicitly ZFEL-like theories in molecular and macroevolutionary theory blunts their critique somewhat. Nevertheless, the prioritization of change does seem to motivate several proposals as to the cause of macroevolutionary diversity, including selection for divergence in related lineages and higher-level selection that favors more diverse clades over more homogeneous clades.

9. A Plea for Pluralism. In the preceding sections I have argued that the traditional and ZFEL-based interpretations of the evolutionary zero-force law both have certain inherent epistemic limitations. Though the ZFEL has certain explanatory advantages, the HW principle remains a viable alternative. I have also questioned the wisdom of relying on forcehood criteria to decisively distinguish between the two frameworks. So how then should we choose between them?

This question prompts a further one: why should we choose at all? Though they share a common epistemic structure, the two interpretations definitively explain opposite sorts of phenomena: one accounts for stasis and the other for change. They also take radically different approaches to the quantitative problem of measuring evolutionary change. The traditional framework focuses on a single, precisely defined property of individual populations. Allele frequencies, or variance metrics derived from them, provide the currency for the various models of drift, mutation, selection, migration, and other evolutionary processes. On the other hand, the ZFEL approach presents two mutually constitutive properties—diversity and complexity—that are not inherently quantitative, but instead can be captured by applying many different variance metrics to many different types of biological ensembles. While the HW principle lays the foundations of mathematical structure for the rest of population genetics, the ZFEL deliberately works at a higher level of generality and leaves these details to be determined by a particular application.

Because of these differences, each of the zero-force interpretations also has a unique epistemic advantage. As things currently stand, the traditional picture has a computational advantage, while the ZFEL has a heuristic advantage. The computational advantage of the traditional view is that the mathematical models of population genetics are built on the foundation of the HW principle. In practice, the epistemic role of these models is something like that of Newton's second law: they provide quantitative predictions of the patterns (including stasis) that result from the interaction of such forces as selection, mutation, and drift. Evolutionary biology currently lacks a comparably comprehensive framework for modeling the interaction of the processes that affect diversity and complexity, though powerful tools do exist for analyzing molecular evolution. McShea and Brandon are aware of this limitation of their framework and provide some suggestions for quantifying the effects of the ZFEL at higher levels of biological organization (2010, 130–31). However, a ZFEL-based system approaching the reach of population genetics is probably still a long way off.

Because the ZFEL provides a more realistic description of actual biological processes, it is much less likely than the HW principle to fail as a null model. There will be many cases in which it is plausible that some observed increase in diversity or complexity is due solely to its activity. In these cases, it will have limited explanatory power unless it can be supplemented with appropriate quantitative tools for decomposing its effects from those of other evolutionary processes. However, this weakness confers a heuristic advantage over the HW principle—when it does fail, the ZFEL is more likely to generate interesting hypotheses to explain observed phenomena. McShea and Brandon provide an illuminating example in their examination of the data on pure complexity throughout life as a whole. The question is not whether the most complex organisms today are more complex than the most complex organisms at the beginning of the history of life; the ZFEL would instead predict an increase in complexity in almost all lineages. That turns out not to be the case, however—while the mean value of pure complexity definitely seems to have increased, the minimum value of complexity seems to have remained stable. There is no reason to think that modern bacteria are more complex than ancient bacteria, though of course it is difficult to say for sure. This suggests some interesting hypotheses: perhaps developmental constraints prevent complexity from increasing in these lineages, or perhaps selection actually tends to act against complexity in the long run.

10. Conclusions. All evolutionary biologists are interested in understanding how the patterns that we see in the history of life can be explained by the interaction of different evolutionary processes. Among these processes, there are some (such as mutation) that are universal among living things, and others (such as meiotic recombination or migration) that are restricted to certain classes of organisms or certain demographic situations. The construction of Newtonian analogies requires biologists to relegate some of these processes to the explanatory background as zero-force conditions, leaving the rest to count as special causes or forces of evolution. This critical decision is the basic point of divergence between rival interpretations of the zero-force law, and it has important implications for the structure of the explanations that result from their applications. Rather than defending either the ZFEL or the HW principle as the unique first law of biology, we philosophers would do better to focus our attention on the criteria by which this decision is made and on their epistemic consequences.

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