Title: Sometimes You Ride the Pegasus, Sometimes You Take the Road: Mitchell on Laws in Biology

Abstract:
Mitchell's philosophical contributions are part of an ongoing conversation among philosophers and scientists about laws and unification in biology, going back at least to Darwin. This article situates Mitchell in this conversation, explains why and how she has correctly guided us away from false idols, and engages several difficult questions she leaves open. I argue that there are different epistemic roles laws (or models describing lawlike regularities) play in biological inquiry. First, they play the role of "how possibly" explanations, akin to Herschel's characterization of Whewell's "a priori Pegasus," and second, they provide descriptions of empirical regularities, akin to the "plain matter of fact roadster."

Key words: laws, unification, integration, explanation, prediction, biology

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Short summary:

This article situates Mitchell's work on laws and integration in historical context and engages a variety of open questions about laws and their epistemic roles in the biological and biomedical sciences, arguing that they play at least two distinct roles.

Bioblurb

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1. Introduction

Most philosophers of biology writing today on the nature of explanation or theory change in biology seem to be more concerned with causation, mechanism, models, and idealization than laws, and far more concerned with "integration" than "unification" (see, e.g., Andersen, 2014a, 2014b, Braillard, P., & Malaterre, C. 2015; Brigandt, 2015; Potochnik, 2017). Indeed, some see talk of laws or unification in biology as of marginal, or perhaps only historical interest. Why? Part of the answer will require a close (but brisk) look at biology itself. Part, however, has to do with a conversation among philosophers and scientists about laws and unification in biology, going back at least to Darwin. Mitchell's (1997, 2000, 2002 2003a, 2003b, 2009) work has played an important role in this ongoing conversation. In my view, Mitchell has correctly guided us away from false idols, though she also leaves some interesting and difficult questions open. Thus, the two central aims of this paper are first, to situate Mitchell's views in this historical conversation, and second, to point to, and begin to address, these open questions. The conversation begins, arguably, with Darwin.[1]

2. Back to the Entangled Bank

In the final paragraph of the *Origin*, Darwin wrote:

> It is interesting to contemplate a tangled bank… and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less improved forms. Thus, from the war of nature, from famine and death,

[1] Though I could have chosen many other scientific figures to begin, I hope it will become clear soon why Darwin is such an apt choice.

> the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. … whilst this planet has gone circling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

Why was Darwin so concerned to characterize his generalizations regarding patterns of inheritance, variability, and growth as "laws"? What was the significance of his comparison of these (rather less secure) generalizations to the law of gravity?

Characterizing these patterns as laws was a deliberate choice, and a key rhetorical move of Darwin's (see, e.g., Hull, 1972, 1973, 1983, 2003; Ruse, 1975, 1979). Herschel was one of the first philosophers of science, and Darwin had read Hershel's philosophical work on the nature of scientific inquiry. So, he knew that Herschel took Newton to be exemplary; in particular, he knew that Herschel viewed Newton as exemplary because of his identification of lawful regularities, resting on observations of "true causes," and his unification of celestial and terrestrial physics. Darwin argues that these laws of variation, reproduction and growth are true causes. Moreover, he argues that if they are in operation, we can see as consequence how the struggle for existence, and thus natural selection, can come about.

It was the latter "hypothesis" that caused Herschel to balk. While Herschel and William Whewell (among the most influential philosophers of the 19th Century) agreed that Newton was an exemplary scientist, they differed about why, and offered rival views about the central methods of science. Herschel was critical of Whewell's celebration of consilience of inductions, or "jumping together of facts," what we today might call inference to the best explanation. In his review of Whewell's massive multivolume tome, *A History of the Inductive Sciences* (1840), Herschel criticized Whewell's championing of methods that he considered less cautious than the trusted path he imagined true scientists ought to take: "The high a priori Pegasus… a noble and generous steed who bounds over obstacles which confine the plain matter of fact roadster to tardier paths and a longer circuit." (Herschel, 1841, p. 223)

From his reading of Herschel, Darwin understood true science to involve the discovery of laws via "inductive methods," and in the *Origin*, he painstakingly recorded observations he and many others had made of patterns of inheritance, variability, and growth. Characterizing these patterns as "laws" was a deliberate choice, as was the reference to gravity.[2] Following Newton's example was – by the lights of both Herschel and Whewell – the mark of mature science. Despite Darwin's choices, however, Herschel and Whewell were both skeptical of Darwin's theory. Indeed, Herschel purportedly called natural selection the "law higgledy pigglety." Why?

Herschel himself never made clear what he meant, but there are ample reasons offered up in the literature (see, e.g. Hull, 1972, 1973; Ruse, 1975, 1979; Hodge, 1977, 1991, 1992; Pence, 2018; Honenberger, 2018). First, Darwin's purported "laws" of growth and reproduction, inheritance, variability, etc., are not exceptionless. Organisms only *tend* to grow to resemble their parents, novel variants arise with *some regularity*, but not in a predictable way (as Darwin said, "by chance"), and *not all populations expand* at a "geometric" rate. Nor are all resources strictly "arithmetical" in their limitations. Moreover, Darwin only argues that *if* these conditions hold – if organisms vary, if variation is inherited, and if resources are limited – *then* competition will lead to natural selection, and in turn, the divergence of character, and adaptation. Strikingly, Darwin does not describe natural selection *per se* as a law, but a consequence, or "result," "entailed," by the general lawful regularities he describes. He grants that these conditions are not always met.

So, Darwin's argument was a combination of what might perhaps be described as generalization by induction, and inference to the best explanation. Darwin's "if-then" claim was the core of his argument in the *Origin*, but he also argues for natural selection as the best available explanation of divergence, biogeography, organisms' stunning fit with their environment, the fossil record, and the many similar structural features and developmental processes among species. Or at least, he argues that this explanation is more probable than special creation. Darwin's reasoning, in other words, was not demonstrative. Not surprisingly, then, Herschel was critical; and he was not alone. Many critics of Darwin (even some of Darwin's "champions") argued that he had at best shown that his explanation was plausible.

Darwin's "laws" lacked the universality of Newton's theory of gravity. Newton himself thought of laws of nature as expressions of God's plan. On such a view, the laws of nature

[2] Thanks to a reviewer for this further information: Hodge has noted that Darwin had indeed considered a "lawlike" program for biology in analogy to Newton but abandoned the "laws of life" formulation in his early notebooks. Another reading of the same passage has "law" playing a role more like "secondary cause" than "Newtonian law," echoing the invocations of secondary causes (and their compatibility with divine design) that Darwin added to the *Origin*'s frontispiece.

cannot come to be, or cease to be. Presumably, God's laws are fixed and unchanging evidence of his providence and benevolence, universal and necessary. Many candidates for "biological laws" lack this character: they are either context-dependent, probabilistic generalizations about systems that are themselves products of history (and, could themselves change if various conditions arise), or they are similar to Darwin's "if-then" claims, describing entailments from sets of initial conditions (many of which are either probabilistic, or, puzzlingly, systematically violated). This has led to a lasting debate both about laws, their role in biology, and the status of biology as science.

3. Situating Mitchell

To situate Mitchell's role in the ongoing conversation about laws in biology, it's first important to be clear about with whom she is in dialogue. Mitchell's contribution to the conversation was, arguably, shaped by the recent U.S. social context in which both evolutionary biology and philosophy of biology, developed. Philosophy of biology as a discipline arose in the mid-twentieth Century, when logical empiricism was declining from its peak, and (at least in the U.S.) the status of evolutionary biology as a science was contested in legal disputes over the teaching of evolution in public schools.[3] So, many philosophers of biology took upon themselves the task of both defining a field of study and explaining and defending evolutionary biology as a science. As a result, many philosophers of biology (Mitchell included) either trained as, or collaborated with scientists, and much of the philosophical work on biology engages with conceptual and methodological debates that arose in scientific practice. For instance, philosophers of biology have contributed to debates among scientists about species, fitness, levels and units of selection, and adaptationism. Mitchell's work is a vivid example of this engagement.

Mitchell and other philosophers of biology brought attention to some important facts about the distinctive subject matter and practice of biological science. Biologists deal with living things on earth, the existence and character of which is both historically contingent, and

[3] For further discussion of the history of philosophy of biology, see, e.g., Ruse, 2018; Malaterre, et. al., 2020. Thanks to a reviewer for these suggestions.

generalizations about are often highly context dependent. So, to achieve something even approaching claims that have the character of "natural necessity" in biology, biologists will often take things to be fixed that they know to vary. If there are anything like "necessary" truths in biology, they are truths that hold under conditions that are highly idealized; that is, they are true only in circumstances that rarely (if ever) hold. Indeed, some such "truths" hold only of impossible worlds – infinite populations, or organisms living in unchanging environments. Yet, biologists seem take several such truths to play important roles in our understanding of biological systems and their evolution. Many function as "as if" organizing frameworks for biological research, or perhaps, as setting out limit conditions, or null models, against which we can test hypotheses or develop explanations.[4]

While the nature of biology and biological science is essential to resolving any debates about laws in biology, there has also been a long conversation among metaphysicians concerning the nature of the commitments of our best scientific theories. While logical empiricists sought to promote relatively metaphysically free science, more recently, philosophers have been more willing to consider laws of nature as central to science. Several philosophers have taken metaphysical questions to turn on whether we ought to treat laws, for instance, as in some sense fundamental, or perhaps instead, universals, properties, or dispositions (Lewis, 1983; Armstrong, 1978, 1983). Mitchell, and most other philosophers of biology, were only indirectly engaged with such conversations. Why? There is a distinctive empiricism and pragmatism at play in much of Mitchell's work, and indeed, the work of many philosophers of biology. Thus, many philosophers of biology do not engage with the questions that puzzle many metaphysicians (should we be Humean about laws, etc.). Such debates do not seem to carry any clear implications, or help resolve, the vast majority of conceptual or methodological debates that arise in the biological sciences. Yet, as I suggested earlier: a central goal of much of the philosophical engagement with the biological sciences in Mitchell's work has been resolving conceptual and methodological questions that arise in the practice of science (see, e.g., Mitchell, 1997, 2000, 2003, 2009).

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[4] Mitchell was not the only one to notice these facts about biological practice. For further discussion of similar views, see also, e.g., Lewontin, 2000; Wimsatt, 2007; Godfrey-Smith, 2006, 2009. Some 'if-then' hypotheticals do the work of null models, equilibrium conditions, or limit cases, what Bill Wimsatt describes as "false models".

Questions about the relative stability of causal generalizations, and the aim and methods of integrative research, do arise in scientific practice. Moreover, concerns about these matters shape practical matters such as law and policy concerning mitigating the effects of climate change, preservation of endangered species, and clinical medicine. For example, clinical intervention requires that one say what cause-effect relationships are relatively stable, given background conditions that themselves vary. The fact of the matter is we often cannot know which such background conditions are in place, making prognosis and treatment enormously difficult. In light of our epistemic limitations, and in light also of the distinctive complexity and contingency of biology, Mitchell has argued, the line between law and accident in biomedicine is not a sharp one (Mitchell, 1997, 2000). So too, not coincidentally, is the line between "natural" kinds and natural enough for a given purpose (prediction, intervention, etc.).

These observations – about both the complexity and contingency of biology – have been a central focus of Mitchell's work. Yet, this contingency has led many to be skeptical of biology's status as a science, starting, as we've seen, with the reception of Darwin's theory. Thus, Mitchell's work has engaged a variety of audiences: not only philosophers, but also scientists misinformed by logical empiricist ideals for science, and the public. To the extent that false presuppositions about the nature of science inform practical concerns, like the teaching of biology in public schools, addressing such matters is important. And at least one such central presupposition is that scientists ought to aim at lawful descriptions of the world. Let us turn now to the details of the philosophical debate this situation has generated.

4. Laws? We don't need no stinking laws!

Many biological generalizations are rather significant, and practically relevant to science, medicine, and law and policy, but we do not give them the honorific status of "laws." Most of us would not say it is a law of nature, for instance, that smoking causes lung cancer, or that extinction is more likely in small, isolated populations. But both are so well established that they are used to support federal laws and policies that govern the advertisement of cigarettes, and the protection of endangered species. Why then do we not call them laws? Philosophers of biology confronting these matters have taken one of several approaches. Some set out normative criteria for laws of nature, and either claim that biology fails to meet them, or meets them in spades.

Others resist setting out necessary and sufficient normative criteria for the status of laws in science. Mitchell's work is an example. Indeed, her work reframes the conversation around laws. Instead of concerning ourselves with what laws "are" (or what criteria they "must" meet), she argues, we should attend to what laws "*do*." That is, she is concerned with the pragmatic and epistemic roles of laws, or lawlike generalizations in biology. Below, I give a brief overview of some of the alternative views in the philosophical literature, situating Mitchell's work in this conversation.

Grasping the first horn (at the normative end of the spectrum), many philosophers have assumed that what is distinctive about laws of nature is their character as empirical, universal, and "necessary" generalizations. Such criteria are assumed to be met in physics; and some have argued that while laws in physics meet the normative criteria for lawfulness, generalizations in biology do not (Smart 1963; Schiffer 1991; Beatty 1995; Earman and Roberts 1999; Woodward 2000, 2001, 2002, 2003; Earman et al. 2002). Others argue that there are two kinds of laws, *ceteris paribus* laws and strict laws, and that only the former are found in the "special sciences" (e.g., biology, anthropology, psychology) (Fodor 1991; Hausman 1992, 133–151; Pietroski and Rey 1995). Others still defend a weaker set of conditions on lawhood and say that laws in biology meet such conditions (Sober 1997; Elgin 2003).

Mitchell's work is an uncomfortable fit with this dialectic. Rather than set out normative criteria for lawhood, she takes a distinctively pragmatic view in this discussion. First, she argues that any account of laws and their role in the biological sciences ought to start with a close examination of scientific practice. Our question should not be whether laws meet ideal criteria, but instead: What *function or role* do candidate biological laws play in inquiry?[5] Second, starting with close attention to practice, Mitchell notes that there are a variety of dimensions along which candidate laws vary – in strength, and stability, for instance. In part on these empirical grounds, Mitchell argues that there is no hard and fast line to draw between purportedly lawful generalizations and accidental regularities. While such views may seem controversial, a close look at the history of debates over laws in biology (along with a careful look at the actual

[5] There is a great deal more to say about the nature of pragmatism and its influence in philosophy of science, and the ways in which Mitchell exemplifies a pragmatic approach to philosophy of science. Suffice it to say that addressing this question in any depth would require a paper by itself. For further discussion, I recommend the following forthcoming: *The Pragmatist Challenge: Pragmatist Metaphysics for Philosophy of Science* edited by H. K. Andersen and Sandra D. Mitchell (2023).

biological sciences, granting we should take science itself seriously as a (defeasible) source of evidence in any such debate), suggests otherwise. Indeed, in many ways, her position seems the most defensible one available. To explain, I will highlight several authors I take Mitchell to be engaging with directly: Beatty, Sober, and Lange.

In Beatty's view, all generalizations in biology are either (a) mathematical, physical, or chemical generalizations, or (b) distinctively biological, in which case, contingent. Beatty's argument is as follows:

- Distinctively biological generalizations describe evolutionary outcomes.
- Evolutionary outcomes are contingent states of affairs; they could have been otherwise, and so do not "proscribe" with necessity.
- Any apparently non-contingent laws of biology turn out to depend for their "necessity" on mathematics, chemistry, or physics.
- Laws of nature must be true, empirical (not mathematical), and "necessary" in the sense of proscribing what's possible.
- Biology's "lawlike" generalizations are routinely violated.
- Therefore, there are no "laws" of biology.

While Mitchell agrees with Beatty that what natural selection yielded may be undone, and, that evolution can lead to different outcomes from the same starting point, she disagrees with his conclusions. The reasons why are as follows. First, she disputes the normative criteria for laws that this picture presupposes; namely, that laws need be universal, let alone "necessary," rather than contingent products of history. While many philosophers have assumed that laws in physics are universal, others still dispute this (Cartwright, 1983; Giere, 1999). Many grant that physical laws hold only given some conditions that restrict their scope, and these ceteris paribus conditions do not prevent laws from doing explanatory and predictive work. Thus, that distinctively biological phenomena are often only true "ceteris paribus," or (in Mitchell's terms) are only (relatively) stable generalizations, it doesn't necessarily follow that they cannot function in the same way as physical laws.

That said, Mitchell agrees with Beatty that we should expect and indeed seek a plurality of mechanisms and causes in biology. Searching for a "unified" theory in biology (the Newtonian ideal) is problematic exactly because the same biological function can be realized in different ways. Indeed, multiple realization is itself a proper subject of investigation of biology; biologists want to understand how and why different organisms have achieved the "same" function, and they do so by investigating different mechanisms, and evolutionary and developmental histories underpinning this "same" function. The unificationist picture presupposes that laws at each level can be reduced to, or explained in terms of, lawful regularities at some lower level. But, in biology, there are biological generalizations about patterns and processes at one temporal and spatial scale that cannot be reduced to generalizations at other scales, certainly not via deductive subsumption. Thus, the presupposition motivating a unificationist picture of science (at least of the deductive subsumption kind) is undermined (see, e.g. Mitchell, 2000, 2003).

What sorts of (lawlike) generalizations are there? Here, it may help to juxtapose Mitchell with Marc Lange. Lange (2005) argues that laws in biology (and other special sciences) describe stable counterfactual generalization, relative to some set of background conditions that (for the purposes of the scope of that discipline) can be regarded as constant. For example, for the purposes of establishing lawlike generalizations in ecology, ecologists treat as assumptions that the sun will not die out, and the seasons will be (relatively) regular. Lange's idea is that the generality of special science laws is always relative to a domain specific set of counterfactual possibilities typical of that home discipline.

In other words, Beatty, Mitchell, and Lange all agree that candidates for law in biology are contingent truths but disagree about the way in which they are contingent, and, whether there is any sharp distinction to be made between laws and accidents. Beatty sees the contingency of evolutionary biology as sufficient to rule out laws in biology. In contrast, Mitchell, and Lange grant that historically accidental generalizations can well count as laws; (indeed, even many physical laws that we treat as "necessary" may well have been otherwise). Mitchell sees different dimensions of counterfactual invariance as matters of degree, whereas Lange draws a sharp distinction between stable and unstable sets (for the purposes of a given scientific field). Lange contends that the special scientists carve out a range of hypothetical circumstances that (for the purposes of a given field), allow us to say what holds (or close enough) under all possible conditions, come what may, no matter what, etc.

Who is right? On the one hand, I agree with Lange that we could (in principle) identify such discipline specific sets of laws – or truths that hold (come what may) given background circumstances we take to be sufficiently stable. In practice, however, disciplinary boundaries are fluid, lawlike regularities are borrowed and redeployed by neighboring fields, and to suppose that we could identify all relevant background conditions for which the laws of a discipline are sufficiently stable is, to say the least, somewhat of an idealization. Stability is, after all, often a matter of degree, and this is especially so when moving between climates, and time scales. For practical purposes, all law-like generalizations in biology are both ”contingent” in the sense of historically contingent on traits and mechanisms that evolved, and contingent on a variety of background conditions, many of which we may well be unaware of. While in principle there are lawful generalizations that hold, provided we hold certain conditions stable, we often simply don't know all the conditions required for the law to count as nomically stable, by Lange's lights. This is why (often) the best we can do is represent the world *as if* they do. Indeed, many "if-then" generalizations like Darwin's regarding natural selection have this flavor: "if these general regularities hold, then we should expect…" (in Darwin's case, natural selection).[6]

Here I think it is worth turning to Sober, another interlocutor in this ongoing conversation. Sober argues that evolutionary biologists derive "if-then" generalizations that have similar properties to laws (they are used in prediction and explanation). Evolutionary theory describes both the "sources" and "consequences" of the causes of evolution. "Source laws" describe general ecological relations between organisms and environments. "Consequence laws" describe the consequences of these relations for evolution. In many ways, this distinction runs parallel to the distinction between what Darwin himself calls "laws" versus "consequences." By way of example, Sober argues that the generalization "heterozygote superiority tends to promote stable polymorphisms" is a consequence law. Overdominance (the selective advantage that accrues to heterozygotes in some environments) leads to stabilizing selection that maintains both alleles in a population (all else being equal). That is, under conditions of heterozygote superiority, allele frequency converges to an equilibrium value of 50:50, irrespective of the initial frequency of the relevant alleles. Sober explains how this kind of "if-then" claim is derived: "When biologists specify a model of a given kind of process, they describe the roles by which a system of a given kind changes. Models have the characteristic if/then format that we associate with scientific laws. These mathematical formalisms say what will happen if a certain

[6] Lange could respond here by arguing that the kind of flexibility that is present in Mitchell's view can be saved on his view by fine graining the "sciences" at issue. Thanks for a reviewer with this suggestion.

set of conditions is satisfied by a system. They do not say when, or where, or how often those conditions are satisfied in nature." (Sober, 1993, p. 16)

Sober's characterization of "laws" requires us to resist some features of "traditional" conceptions of law but satisfies others. It tells us what (all else being equal) will ensue, much like Darwin's "if-then" conditional in the *Origin*. To be sure, what such "if-then" conditionals describe is often a highly idealized circumstance; in this case, we must assume that no other factors than natural selection for this heterozygote type are at work in a given population – no countervailing selection for other traits, no migration, or drift, or the effects of sampling error, on the distribution of gene frequencies. The models Sober is describing give us something like "necessity," provided such conditions hold. For instance, under the presuppositions above regarding overdominance, a 50:50 distribution of alleles would necessarily come about (even though such conditions may never be met!). Sometimes Sober seems to suggest that the conditions of the model need never be met for the if-then generalization to be true. Sober gives the example of the Hardy-Weinberg theorem and compares it to a proposition about coin tossing.

There is something right about this, and something wrong. Hardy-Weinberg is a theorem, which states that, if a population meets certain conditions, it will be in equilibrium. Theorems are (by definition) necessary truths. But they are not merely "mathematical" truths; they are not true *only* in virtue of the truths of mathematics. Rather they are (or would be) true any system in which the conditions of the model hold. Hardy-Weinberg's equation is a description of a system where populations are infinite. There are no infinite populations. However, we can (and do) use the theorem to derive empirical claims about how populations are in fact (i.e., empirically) subject to, e.g., mutation, selection, or drift. That is, the model serves as a "null" model, which biologists use to derive empirical hypotheses about the various ways in which populations depart from the conditions set out in the model.

Many theorems in biology – and evolutionary theory in particular – have this character. For instance, in 1930, Fisher formulated the Fundamental Theorem of Natural Selection: 'the increase of average fitness of the population ascribable to a change in gene frequency . . . is equal to the genetic variance in fitness' ([1930], p. 377). He compared this fundamental theorem to the second law of thermodynamics, and claimed it provided the fundamental basis of evolutionary change. Yet, he shortly thereafter remarked on how this generalization is systematically violated, namely, where environments are in flux. As Okasha points out, this only means that the FTNS "properly understood" is true, given Fisher's qualification "'due to natural selection in a constant environment'... Without the qualification the FTNS is simply untrue—for it implies that selection must always drive the average population fitness up, which… is false" (Okasha, 2008, p. 330). What function then does such a false claim about an imaginary situation serve? Environments change all the time!

Like many such theorems in theoretical biology, the FTNS describes the preconditions on some pattern or process. Fisher's claim is that any evolutionary change by natural selection requires the presence of a reservoir of additive genetic variance. While this may not seem so stunning to us today, Fisher's demonstration did important work for evolutionary biology, at least at the time. One of Fisher's lifelong goals was to answer many of Darwin's detractors. Skeptics of natural selection were concerned that variation would be effectively lost in each generation. Starting with his synthesis of Mendelian and Darwinian theory in 1918, Fisher sought to show that, on a particulate theory of inheritance, variation would not be lost in every generation, and natural selection *could be* sufficient to generate change in populations. The Fundamental theorem was a natural continuation of this work. With the theorem, Fisher was concerned to demonstrate the exact conditions under which variation could yield cumulative change over evolutionary time scales. His theorem was thus, in a sense, a further development of Darwin's "if-then" conditional: Provided additive genetic variance is in place, natural selection can generate adaptive evolutionary change (cf. Plutynski, 2006).

Sober identified some mathematical results in biological theory that play important roles in setting out the conditions on any explanation in evolution. While Hardy-Weinberg and the Fundamental Theorem come as close as possible to "natural necessities" in biology, it's not clear they should be called "laws." Mitchell takes laws to support predictions, and to function centrally in explanations, and to have varying scope, strength, or stability. Fisher's Theorem does not have any direct predictive power, though it may have something like "indirect" explanatory power. Theorems or results such as the examples Sober describes (e.g., the 50:50 overdominance case, or sex ratio cases) function as what one might call "organizing frameworks" for biology. Birch (2017) argues that Hamilton's rule is one such case – the rule that allows biologists to predict and explain when biological individuals are likely to sacrifice their own immediate needs for near relatives. Such theorems, principles, or "rules" provide conditions on any evolutionary process or set out truths that hold necessarily for any system that meets the conditions set out in the model. Such theoretical results play an important role in biology, just as Darwin's algorithmic argument for the application of "Malthus's law" to the natural world. If organisms have heritable variation, and resources are limited, then competition will necessarily change these populations over time.

When generalizations take the form of theorems, what exactly is their status? Mitchell (1997) urges us to consider what functional role a candidate law plays in scientific practice, rather than whether it meets some normative conditions widely believed to be required of laws. She thus provides a way of disposing of this dilemma. By inviting us to focus on the *function* of law-like generalizations, rather than their normative criteria or standing as laws, we can see how the sorts of theorems we've just described play a distinctive functional role in biological inquiry. Unlike the kinds of contingent generalizations typically identified as candidate laws in biology, which function in prediction and explanation *ceteris paribus* (e.g., Kleiber's rule), we might characterize these as "organizing principles," which frame future research, setting out the conditions on various processes or likely outcomes, offering "how possibly" explanations, or setting out null conditions against which we test hypotheses.

Mitchell describes several "dimensions" of scientific laws: they are more or less strong, stable, specific, and have wider or narrower scope:

> … scientific laws describe our world, not a logically necessary world… All laws are logically contingent, and yet there is still a difference between Mendel's law of 50:50 segregation and Galileo's law of free fall. How can we represent that difference?... it is not the difference between a claim that could not have been otherwise (a "law") and a contingent claim (a "non-law"). What is required to represent the difference between these two laws is a framework in which to locate different degrees of stability of the conditions upon which the relation described is contingent… The difference between generalizations in physics and those in biology is inadequately captured by the dichotomy between necessity and contingency. They could both have been otherwise. What it would take to make them otherwise is different. They, therefore, have different degrees of stability (Mitchell, 2000, p. 243).

There is a sense in which the theorems I've described are different merely in degree of stability from other laws. So, it's not clear exactly how to situate these in Mitchell's picture. Perhaps they are not candidate laws, on her view. Yet, it seems that they function in a way that is key to the explanatory enterprise of biology. So, an open question that Mitchell leaves unanswered is exactly how to understand the role of these "if-then" claims. They do seem to play an important role in explanation and so function akin to laws, but not in the same way as more or less stable laws of the sort Mitchell describes above. For Mitchell, these laws are not stable at all: As she argues, "In the multi-dimensional space defined by the multiple aims of scientific practice including the ontological parameters as well as degree of abstraction, simplicity, and cognitive manageability, it may well turn out that all or most of the generalizations of physics occupy a region distinct from the region occupied by generalizations of biology... The conditions upon which physical laws are contingent may be more stable through space and time than the contingent relations described in biological laws." (2000, p. 263). Indeed, one of Mitchell's insights is that it exactly because of this high degree of contingency that biologists are required to idealize, and it is because of the great complexity of the causal explanations in biology that they appeal to several different idealized models in explaining.

5. Integration, not Subsumption

I've argued that Mitchell's views on laws open up the possibility to consider a range of more or less contingent, stable, or idealized representations of biological systems and their predictive and explanatory roles. What is the relationship of this view to her larger views on integration, as opposed, for instance, to deductive subsumption? In contrast to the view, according to which laws of nature describing patterns and processes at one temporal and special scale are deductively subsumed by others, integration involves the sharing of data, models, and tools across disciplines. Biology is one domain where deductive subsumption has been nearly absent, but integration is rampant. Mitchell's work has drawn attention to the significance of integration in biology and emphasized that this integration is compatible with a pluralist, rather than a reductionist view of scientific progress and explanation. How does this go?

Idealized models describing conditions on, or "if-then" claims about, biological patterns and processes are often developed the service of explaining patterns across outcomes that are similar in relevant respects. What explanatory "if-then" biological generalizations do is tell us what the biological explanation would be (under various often highly idealized conditions). For instance, we can say (all else being equal) that cancer treatment is more likely to fail under some conditions versus others. Clinical intervention requires that one can say what cause-effect relationships would hold, as well as which ones are relatively stable, or likely to be, given likewise relatively stable background conditions.

Cancer researchers may not know all relevant background conditions for any class of lawlike generalizations; indeed, often they do not. Nonetheless, such generalizations can be key to helping us better understand and intervene on a disease that is notoriously heterogeneous and complex. By way of example: Why should we expect treatment to fail sooner in people with larger tumors? Here's an answer: If we know that mutations are drivers of resistance to treatment, and a population of cancer cells in a tumor is dividing at a regular rate, with a mutation rate per cell division of u, we know that the larger the tumor, the more mutations are generated, and the higher the value of u, the lower the tumor size at which treatment fails. (Of course, the assumptions of this model are strictly speaking false: not all cells in a tumor divide at the same rate, nor to all mutations or mutation types arise at the same rate. But it is true (enough) that this is one central reason why chemotherapy fails sooner in larger (more advanced) cancers, all else being equal.

Here is an instance where the same general mathematical model that is used to predict various evolutionary outcomes can also be used predict at what point cancer treatment will fail, given a certain number of rounds of different kinds of drugs. The higher the mutation rate, the lower the advantage gained from adding further drugs. In such cases, what is being explained is a "general" pattern or expectance, given some initial conditions we know to be in operation in every cancer. I would argue that this is a vivid instance of the kind of "integrative" research Mitchell has described.

Biologists often borrow models, theories, and principles, from one domain, and apply them in another. Identifying common problems, or similar patterns, across such domains is sometimes used to generate theoretical models that can be borrowed and reapplied elsewhere. Other times, biologists draw about theory, evidence, and tools and technologies from neighboring fields to solve common problems. The latter is more akin to the "roadster work" of gathering as wide a domain of evidence as possible to arrive at some general conclusion.

Such an integrative approach is, Mitchell argues, compatible with a pluralist, rather than reductive, unificationist approach to science. Historically, philosophers of science imagined that explanation and scientific progress went hand and hand, following a common method of deductive subsumption of lawful regularities (see, e.g., Nagel, 1961). Mitchell brought attention to the fact that biologists recognize that the same phenomena can be approached and explained in different ways, deploying different models, and explanatory frameworks. An integrative explanation is one that draws upon all these diverse frameworks, and rather than reduce one to another, embraces several as part of a single, integrative explanation. This is a distinct strategy from the unificationist approach, which takes the aim to be reduction via deductive subsumption. There are many instances of this kind of integrative approach Mitchell has described in her own work, but one vivid example is explanations of the division of labor in an insect colony. On Mitchell's view, explaining this pattern requires appealing to multiple, idealized models, no one of which is simply reduced to or eliminated in favor of the other, and each of which identifies important causal factors of relevance to the pattern observed:

> … given the multiplicity of causal paths and the historical contingency of biological phenomena, the type of integration that can occur in the application of models will itself be piecemeal and, to varying degrees, local. The result is that pluralism with respect to models can and should coexist with integration in the generation of explanations of complex and varied biological phenomena. (Mitchell, 2003a, p. 68)

This integrative approach, which embraces the plurality idealized models in science, has gone on to inform much of the current conversation regarding the role of idealizations in science, and the embrace of pluralism and diversity of models (see, e.g., Potochnik, 2017; Ludwig, D., & Ruphy, S. (2021).)

6. Conclusions:

Mitchell's work has led us away from the false idols of universal generalizations, and unifying, reductive explanations. Her pragmatic perspective leads us to refocus our attention on what biologists *do*. When we go and look, we see an array of scientific inquiries and practices; there are lawlike generalizations do in biology, which function in prediction and explanation. There are also theorems, theoretical principles, and "null" or "limit condition" results of biology. I've argued that many "would promote" or "if-then" statements and theorems in biology do have a status akin to "natural necessity," in that they describe true, empirical generalizations about any population that instantiates the properties described such models. These may function in explanation as giving the "baseline" conditions, limit case, or necessary conditions on some class of outcome or process. There is room for both the roadster and the Pegasus – for inductive generalizations about contingent biological patterns and processes, and for theorems about idealized populations and their necessary properties.

Mitchell's argument that there is no hard and fast line to draw between the lawful and merely contingent captures the fact that in biology, we often only expect but do not know which background conditions are in place, or even which ones are relevant, to the stability of various generalizations. Sometimes, as Lange suggests, we can list the domain specific background conditions assumed to hold. While in principle, we could set out all the relevant conditions on stability of laws in any domain, in practice, we often simply do not know which conditions our generalizations are contingent on. So, in the face of uncertainty, we either take the road, or ride the Pegasus: we either gather data and carefully document general "laws", or we set out what would in theory come about, if certain conditions were in place.

This, in essence, was the balance Darwin was trying to strike in the *Origin*. On the one hand, he had discovered important patterns – or, lawful regularities of generation and growth, variation etc. Darwin was able to document these general facts, based on observation. However, Darwin also summons Whewell's Pegasus. When he appropriates Malthus's law and argues that if there are "arithmetic" limits to natural resources, and organisms tend to reproduce "exponentially," then a struggle for existence, and natural selection will necessarily result. Thus, Darwin did discover something akin to a "law" in the sense of a "necessary" truth of biology. For his purposes, what was important was that the initial conditions he described were common or plausibly in operation across a variety of cases, not that they were universal. It seems that the contingency and complexity of biology means that one can only arrive at necessity when things are held fixed that are known to vary. So, for practical purposes, the line between law and contingency in biology and biomedicine is not a sharp one, as Mitchell has argued, even if in the imaginary worlds of metaphysicians, we could draw such boundaries.

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