Euro Jnl Phil Sci (2018) 8:435–454
https://doi.org/10.1007/s13194-017-0194-0

ORIGINAL PAPER IN THE HISTORY OF PHILOSOPHY OF SCIENCE

The economy of nature: the structure of evolution in Linnaeus, Darwin, and the modern synthesis

Charles H. Pence[1] **· Daniel G. Swaim**[2]

Received: 6 April 2017 / Accepted: 21 November 2017 / Published online: 6 December 2017

Abstract We argue that the economy of nature constitutes an invocation of structure in the biological sciences, one largely missed by philosophers of biology despite the turn in recent years toward structural explanations throughout the philosophy of science. We trace a portion of the history of this concept, beginning with the theologically and economically grounded work of Linnaeus, moving through Darwin's adaptation of the economy of nature and its reconstitution in genetic terms during the first decades of the Modern Synthesis. What this historical case study reveals, we argue, is a window into the shifting landscape of the explanatory and ontic uses of structural concepts. In Linnaeus, the economy of nature has both ontic and explanatory import; in Darwin the ontic and explanatory aspects start to come apart (with the explanatory aspect being foregrounded); and finally, in the Modern Synthesis, the economy of nature is replaced by the conceptual toolkit of population genetics, the structural elements of which are nearly entirely explanatory. Having traced a historical trajectory of structural concepts that moves from an ontic formulation to an increasingly explanatory one, we conclude by outlining some insights for structural realism.

Keywords Economy of nature · Carl Linnaeus · Charles Darwin · Sewall Wright · Ernst Mayr · Ecology · Modern synthesis · Population genetics · Structural realism

✉ Charles H. Pence
charles@charlespence.net

[1] Department of Philosophy and Religious Studies, Louisiana State University, 102 Coates Hall, Baton Rouge, LA 70803, USA

[2] Department of Philosophy, University of Pennsylvania, Claudia Cohen Hall, Room 433, 249 S. 36th Street, Philadelphia, PA 19104-6304, USA

1 Introduction

Recent philosophy of science, especially that centered in the philosophy of physics and the debate over realism and anti-realism, has been drawn toward the pursuit of *structure.* Much work has been devoted to various formulations of both *ontic structural realism* (OSR; Ladyman and Ross 2007; French 2014) and *epistemic structural realism* (ESR; Worrall 1989; Ladyman 1998),[1] two competing positions describing the ways in which structures and their properties constrain what it is that our best scientific theories tell us about the world. The elucidation of these views has significantly altered the landscape of the scientific realism debate as a whole. Further work has looked at the interpretation of structure in particular sciences (such as quantum field theory; see French and McKenzie 2012), the way in which we should characterize structure itself (van Fraassen 2006), or how we should understand the relationship of "grounding" or "fundamentality" that putatively holds between objects and the more fundamental structures which underlie them in OSR (French 2010).

One distinction present early on in the development of scientific structuralism, however, has fallen away in recent literature. In a seminal paper, Ernan McMullin (1984) notes that when we study structure as deployed in the sciences, we must be careful to separate two roles which it might play. One, which we will call the *explanatory* role, involves identifying structures as salient features of the explanations for phenomena in the sciences – without weighing in one way or the other on the metaphysical or ontological status of those structures. Another, which we will call the *ontic* or *metaphysical* role, involves positing that structures really, genuinely exist in the world, and that our best scientific theories are providing us with information about them.[2]

Notably, this is not the same distinction as that between the ontic and epistemic forms of structural realism (similar as the terminology must unfortunately be). ESR is a claim not about the role of structures in explanations, but about what kinds of beliefs we are warranted in drawing from a given, successful scientific theory – namely, we are warranted only in believing the theory's structural content to be a true (or an approximately true) representation of the world (for more on this distinction, see Ladyman 1998). Rather, McMullin is attempting to analyze a pattern arising from the history of science itself. Scientists in geology, chemistry, and biology, among other fields, have pointed to structures as significant parts of the theories which they have proposed. In McMullin's words, "in many parts of natural science, there has been, over the last two centuries, a progressive discovery of *structure.* Scientists construct theories which explain the observed features of the physical world by postulating models of the hidden structure of the entities being studied" (McMullin 1984, 26). If this is true – and we will offer here yet more evidence that it is – we are left with an important analytical question: are these structures merely explanatory devices (perhaps, even, idealizations or fictional models; Bokulich 2016; Morrison 2014), or are

[1] Ladyman is not here offering an endorsement of ESR, but instead a very clear explication of the content of the view. See Ladyman and Ross (2007, pp. 124–129) for an especially nice reconstruction of ESR, and a pointed argument against it (and in favor of OSR).

[2] A similar separation between metaphysical/ontic and epistemic/explanatory roles has been made in the case of the scientific models literature by Rohwer and Rice (2016).

they intended to represent structures which actually exist in the world? In short, are they filling the explanatory or the ontic role?

McMullin, for his part, argues that the two roles are in fact connected. More than this, he claims that we can support a version of realism using that connection: the success of the explanatory role of structure serves, he argues, as evidence (even if only of a tempered or mediated sort) for the success of the ontic role of structure, at least in certain fields. As he puts it, "the explanatory power" of a given structural hypothesis, "its steadily improving accuracy, gives good ground to suppose that something can be inferred about real structures that lie far beneath us" (McMullin 1984, 28).[3] It is precisely the connection between the ontic and explanatory roles for structure that we wish to explore here, in the context of the biological sciences.

It is clear that this relationship has important bearing on the concerns of contemporary structural realists. If these structures are successfully playing an ontic role, then this seems to provide at least some comfort to the supporter of OSR (McMullin himself, for example, took it to support some version of structural realism, though the relationship between his view and OSR is unclear). But if structure in a given theory is merely an explanatory device, and has no metaphysical or ontic purchase, then at the very least that structure is of no help to a project like OSR, and examples of such structures may serve as cautionary tales that help us more clearly define the limits of applicability of OSR as a general approach to scientific theories. We claim that the history of evolutionary biology offers us (at least) one particularly interesting example of such a case.

It is notable that the pursuit of structure so common in the philosophy of science more generally has broadly passed over the biological sciences. McMullin himself makes a passing reference to the "elegant example" of the gene as a concept whose realist import should be cashed out structurally (1984, 28), but beyond this possibility, which has not been developed, biology was left out of the shift to structures by philosophers of science until quite recently.[4] We will pursue an example here which spans what we claim is an underappreciated instance of theoretical continuity in the biological sciences. The concept of the *economy of nature,* forming as it did a background, *structural* element in the works of Linnaeus and Darwin, seems to be held at least somewhat intact throughout a dramatic series of theory changes. When we pursue it through the development of genetics and the Modern Synthesis, we find that while the set of features of the world taken to underlie this set of structural explanations changes almost beyond recognition, the structural explanations, and thus the explanatory role of at least some sort of structure, remain. We thus have a case study which offers an example of a group of structural explanations which persists across a wide variety of theories, vastly different in their other scientific, philosophical, and even theological assumptions, making it a perfect case to explore the interplay between the ontic and explanatory roles for structure.

[3] As an aside, it is difficult to discern exactly what McMullin's own views on the ontic role for structure are, as he (perhaps intentionally) keeps his metaphysical commitments tentative. He says, for example, that structure is "taken to account casually for the observable phenomena" (1984, 26), and that structures "provide an increasingly accurate insight into the real structures that are causally responsible for the phenomena being explained" (1984, 30), but also rejects the claim that "acceptance of a scientific theory involves the belief that it is true" (1984, 35).

[4] The absence of McMullin's article from the references of both Ladyman and Ross (2007) and French (2014) is remarkable.

We start, in the second section, by considering the works of Linnaeus, including the intellectual context which inspired them. Linnaeus's invocation of the economy of nature (hereafter EoN), we will claim, is both ontic and explanatory – structure exists in the world, in at least some important sense prior to the entities (organisms and species) which constitute it. Section three turns to the ways in which Darwin picks up on these themes in Linnaeus. Darwin has a more difficult – perhaps, as we will see, even confused – relationship to the ontic and explanatory uses of the EoN, as he rejects Linnaeus's theology. The fourth section pushes these considerations into the period of early genetics and the Modern Synthesis where, we claim, the ontic role is entirely shed, and the genetic structures which take the EoN's place are seen only as an explanatory tool. We conclude by engaging the broader question we raised above: what does this ebb and flow of the ontic role for these structures say about their status in the life sciences, and how can we use this example to illuminate the general question of structure in scientific theories?

2 The economy of nature and the works of Linnaeus

It will become apparent as we move through our historical cases that the EoN, as a concept, has no one, fixed definition. Even so, it can be helpful to sketch a general picture of the notion, and then see what variations on this central theme emerge.

The fundamental idea underlying the EoN is that of ecological *affordance,* a structure of ways of interacting with the environment, each of which can potentially be utilized by an organism. Pearce (2009) shows that this broader idea is expressed more particularly in terms of natural *stations* and *places* in the works of Linnaeus and Darwin, respectively. 'Station' is taken to refer to the structure of the natural world conceived of as largely static and inanimate, whereas 'place' refers to ecological space conceived of as changing, living, and dynamic. Our claim, then, is that the notion of *affordance* offers a concise way of describing what each of these more specific expressions have in common: that the ecological nodes in the EoN are "out there" (in a sense to be described in more detail for each author below) to be exploited by organisms, and that different organisms will be differentially successful in doing so. Nodes within the EoN afford for the success of organisms, whether conceived of as static or dynamic.

Let's turn to our first example, to be found in the works of Linnaeus. While we take the intellectual roots of Linnaeus's thought to have two key aspects (a theological and an economic one), it is the theological that most clearly supports Linnaeus's commitment to the EoN. Our first task, then, is to trace some of the history of the theological underpinnings that ultimately frame Linnaeus's views, so as to illuminate them more fully.

The influence of theology on biological work throughout the European continent is apparent as early as the mid-seventeenth century. Jan Swammerdam's 1669 preformationist theory of development takes a heavily theological tilt, to the extent that he argues that "the entire human race already existed in the loins of our first parents, Adam and Eve," and claims that the "ideas and types" embedded in embryological material are essentially "rational" (Richards 2002, 211).[5] In the 1750s, Albrecht von Haller's theory

[5] It seems plausible that to call germinal fluids "rational" supports the notion that the natural world contains essentially structural elements. God, after all, is (usually) taken to be *essentially* rational, and here it may be understood that the world is "pre-structured" to reflect God's image in this way.

of epigenesis posited a “formative force” that guides the development of organisms from the earliest embryonic stages all the way through the maturation of adults (Richards 2002, 213). Fellow Swiss embryologist Charles Bonnet adopted a similar view, ascribing to God in particular the force that sets the “multitude of germs” along their developmental paths. Bonnet’s conception is a progressive one, wherein the natural development of the germinal types is toward a “higher perfection” (presumably preordained by God; Richards 2002, 214).

There are differences in the precise dimensions of each of these writers’ thought even in the handful of examples just mentioned. But there is a unifying theme that seems to bind them: namely, the widespread belief in the notion that the world is replete with some sort of structure, and, moreover, that this structure issues from God’s rational intellect (or something near enough). Clearly, the general theological milieu of seventeenth and eighteenth century Europe made appeals to divine providence eminently plausible even for natural historians and well-informed men of science. Barry Gale (1972) shows us that this can be glimpsed in thinkers as diverse as Goethe, Patrick Matthew, and Buffon. According to Goethe, “The animal is formed by [environmental] circumstances: this explains the inner perfection and its expediency with regard to external conditions” (Gale 1972, 328). For Goethe, that organism and circumstance appear so well-fitted, one to the other, is due to the rational order manifest in nature, and for him this order has clear theological roots.

This commitment to the notion of a rationally structured world makes it easy to see why it would have been commonplace to speak of nature as an economic order. *Economy*, as a concept, is rooted historically in the Greek *oeconomia*, which is usually understood as denoting something like the art of “household management” (Schabas 2005, 3).[6] Although Linnaeus’s precise expression of nature’s economy is given in terms of a static structure of natural stations, it is certainly not the case that the EoN had always been so conceived. Hanns Reill argues that in this seventeenth- and eighteenth-century period, just when explicit reference to nature as an economic order is becoming the norm, we see a shift away from the idea of the world’s harmonic balance as static, toward a conception that is fluid and dynamic (Reill 2005, 89). This plays nicely with the root idea of “household management,” since humans are nothing if not fluid and dynamic (as anyone with children will attest).

But the world’s being seen as fundamentally fluid and dynamic does not, in this period, undermine one’s license to claim that it is intelligible. The world was, indeed, considered to be so thoroughly intelligible that it was frequently asserted that human economics could be modeled after the economic order of nature. Goethe, for instance, attempted to model the budgets during his administration of the Saxe-Weimar-Eisenach duchy, to the extent possible, on what he called “natural budgets,” which are “inviolate balances” in nature’s perfect economy (Jackson 1994). In an essay on Adam Smith, Margaret Schabas (2003) argues that Smith probably understood value in much the same way as other “subtle or imponderable fluids” in the physical sciences. There is a natural sense, for Smith, according to which value “fixes or realizes itself within some subject,” as do heat or other chemical properties, reflecting the widespread contention

6 See also Pearce (2009, 499–500) for a nice analysis of the original Greek conception of *oeconomia*. Koerner (1999, 81–85) also shows that Linnaeus was given to taking up this metaphor of “household management” to illustrate his notion of nature’s self-regulatory character.

that the world in general can be understood to be transparent to the human mind, and so used as a metrical device for human endeavors (Schabas 2003). That is, even though the world's structure is fluid, it still generates intelligible signals that enable us to fashion our human endeavors after the model impressed on nature by the intellect of God.

This interplay of conceptual forces is readily apparent in the work of Linnaeus, in two dissertations entitled *Oeconomy of Nature* (Linnaeus 1762, 39–129) and *Police of Nature* (Linnaeus 1781, 1:129–66).[7] Linnaeus was, as it happens, not only an important figure with respect to the formalization of natural history and taxonomy, but also in Swedish economics (Schabas 2005). His particular brand of economic thought was closely tied to protectionist cameralism, seeking to establish a fully self-sufficient Swedish state that could stand without need of imports. As with others working at this time (and before), Linnaeus thought that the economic order of the state and that of nature should essentially reflect one another in their structure. This is due to Linnaeus's theologically rooted conviction that the world is basically intelligible in its structure, though here conceived of as static. He writes in *Police of Nature*:

> Thus we see Nature resemble a well regulated state in which every individual has his proper employment and subsistence, and a proper gradation of offices and officers is appointed to correct and restrain every detrimental excess. (Linnaeus 1781, 1:164)

God has *imprinted* onto nature, according to Linnaeus, a perfect economic order, and that order is fully self-regulatory. Each creature is circumscribed within its particular role and subsists on some particular kind of food, and insofar as these boundaries are transgressed and excesses of whatever sort become detrimental to the plenary order, the EoN is capable of regulating and correcting such excesses such that everything is returned to its proper place in the broader balance of things.

The EoN, of course, does obvious conceptual work in Linnaeus's *Oeconomy of Nature*. But it does some heavy lifting in other contexts, too (even if only indirectly). The binomial system of classification developed in the *Systema Naturae* makes obvious the need for a basically intelligible structure manifested in the world. Even though Linnaeus understood his classificatory system as "artificial" rather than "natural" (that is, a reflection of the convenience of certain concepts with respect to human intellectual capacities rather than a true depiction of nature), he still held that some manner of natural structure really exists (Wilkins 2009, 70–75). One might plausibly interpret the *Systema Naturae* in the same vein as the contemporary idea of "partial truth." If a taxonomic system such as his can be taken as even a partial mapping of natural groups in the biological order, this seems to presuppose that the biological order has a fundamental, preexistent structure.

[7] "Dissertations," in eighteenth-century Sweden, were, as we learn in the preface to one translated collection, "the works of the most capital disciples of [Linnaeus's] school, composed under the direction of its illustrious founder Linnaeus, and very frequently dictated by him" (Linnaeus 1781, 1:v–vi). Thus the *Oeconomy of Nature* dissertation, listed as by one "Isaac J. Biberg," was dictated to Biberg by Linnaeus, and likewise with the *Police of Nature.* This question of authorship is illuminatingly explored by Stauffer (1960, 239). The two editions cited are the English translations read by Darwin; the translation of *Police of Nature* is unfortunately highly abridged by the translator.

The EoN is central to Linnaeus's elucidation of this structure. He writes in *Oeconomy of Nature* that:

> By the Oeconomy of Nature, we understand the all-wise disposition of the Creator in relation to natural things, by which they are fitted to produce general ends, and reciprocal uses. […] Whoever duly turns his attention to the things on this our terraqueous globe, must necessarily confess, that they are so connected, so chained together, that they all aim at the same end, and to this end a vast number of intermediate ends are subservient. (Linnaeus 1762, 39–40)

Place this beside the quote above relating the natural structure of the world to the structure of a well-regulated state. For Linnaeus, close observation reveals a general picture of reciprocity with respect to ends and uses in nature. The organic world is "chained together" by connections that serve to promote the function of the whole, and the end of the whole of nature is the maximal benefit of God's creatures. But this can only be made intelligible, according to Linnaeus, by then positing that there are specific "stations" in nature, certain "offices" that certain types of organisms can be said to occupy, forming a structure that is, therefore, analytically prior to the basic function of nature, and also largely immutable. This becomes even clearer when Linnaeus speaks in terms of the *Polity* of nature, somewhat loosely analogous to the idea of "police" (Rausing 2003, 175).[8] This should not be confused with the notion of police that we might glean from the contemporary use of the term. As Lisbet Koerner (1999, 82–3) makes clear, Linnaeus's conception of *policing* is tightly related to his broader conception of "divine economy."[9] So while the maintenance of nature's economy requires something that performs the task of regulation, regulation is here understood as the performance of certain functions for the greater benefit of the natural order, and not in terms of exercising force. For instance, Linnaeus claims that certain types of insects can be understood as the "police" of nature, ridding the world of certain "detrimental excesses" (Worster 1977, 45).

For Linnaeus, then, there is a clear sense in which the EoN plays the ontic, in addition to the explanatory, role. That is, the EoN is such that there really are particular "stations" in the world that certain actors are created to occupy, and these stations are revealed by study of the natural world. This fits quite comfortably with a picture of nature that is closely wedded to theology. God, as architect, would plausibly have laid down a fundamental structure for biological reality before creating the creatures that occupy a given structural niche.[10] But, whatever the case theologically, Linnaeus sees the basic concept of the EoN as one with explanatory and ontic import. Indeed, for Linnaeus the explanatory role is largely *parasitic* on the metaphysical role. Because God has imprinted the world with an intelligible structure of affordances given in terms

[8] For an illuminating analysis of the "polity of nature" idea, see Pearce (2009).

[9] Koerner cites (and quotes) a sermon delivered by Linnaeus (1763), which was given in the form of a "eulogy to animals." He attempts to image a "world without beasts," and claims that without them the world could not properly regulate itself.

[10] Notably, to avoid straying too far into the history of ecology, we will for the purposes of this paper bracket discussion of the term "niche" as a potential further locus where the "economy of nature" (or, more precisely, the concept of "places" within the economy of nature) might find its way into the history of evolution. We will briefly return to ideas arising from the history of ecology in section 4.

of natural stations, a keen observer (such as Linnaeus) is in a good position to explain the basic function of nature: the maximal well-being of creatures. The same facts even enable analogical extensions of this reasoning, such that, for example, human economics can also be explained and modeled in terms of the structure evinced by the EoN.

Even though its origins lie well beyond the boundaries of natural history proper, the EoN is doing a great deal of work for Linnaeus, and clearly informs his broader perspective on the basic intelligibility of nature. Through his understanding of the EoN, something important to the history of science is glimpsed: a relational structure of reciprocal means and ends that form a functional chain to promote maximal well-being for God's creatures. The theological trappings are soon to be done away with, but the structural explanations in which the EoN appears will remain, as we shall see.

3 The economy of nature in Darwin

Given the twin roots of the EoN in Linnaeus's theological convictions and Swedish economic policy, it is perhaps surprising that it is found throughout Darwin's work, Darwin being neither theologically inclined nor Swedish. But the concept appears early and often. Darwin read Linnaeus's *Police of Nature* on the 8th of May, 1840, and the *Oeconomy of Nature* on the 13th of May, 1841 (Darwin 1859, 10v, 11v). The early 1840s are an interesting moment in the development of Darwin's theory. The two mechanisms which Darwin would continue to cite as responsible for natural selection, differential reproduction and the inheritance of acquired characters, appear together first in late November of 1838, in the N notebook (Darwin 1838c, N 42), and the three core principles of natural selection – heritability, variation in fitness, and Malthusian superfecundity (the geometrical increase of population, faster than any possible arithmetic increase in the food supply) – are in place on or just before the 2nd of December (Darwin 1860, E 58).[11] Darwin then turns to the packaging and presentation of his theory as publishable, public science. While there is an intriguing gap of four years here, between the essentially complete formation of the theory in the notebooks and the preparation of the *Sketch* in 1842,[12] the *Sketch* contains the EoN in essentially all the forms in which it would be found in Darwin's mature works. Darwin even describes the entire second part of the *Sketch* – corresponding to the last seven or so chapters of the *Origin,* in which Darwin considers both objections to and unexpected results which follow from common descent and natural selection – as "devoted to the general consideration of how far the general economy of nature justifies or opposes the belief that related species and genera are descended from common stocks" (Darwin 1909, 121).

For Darwin, then, what role does the EoN play? It would be surprising if it were grounded in the very same facts as it is in Linnaeus's case, since Darwin did not want to invoke a divine plan of creation in the natural world. But that does not mean, a priori,

[11] Completing the standard picture of selection in the *Origin,* Darwin adds the analogy with artificial selection the following week (Darwin 1860, E 63). For more information on this pivotal period, see Ospovat (1981) and Hodge (2009b). Stauffer also summarizes many of the relevant sources for Darwin's use of the EoN (1960, 235–36).

[12] While much ink has been spilled over the putative reason for this seeming cessation in Darwin's work (see helpful discussion in Ruse 2009), this need not concern us here.

that the EoN could not play the ontic role for Darwin. Further, we have yet to see exactly what kind of explanatory role it plays for him. When we unpack the historical narrative here, we will see that Darwin's use of the EoN is unstable, retaining the EoN's explanatory use throughout his theorizing, but demonstrating an uncertain commitment to its ontic role.

Darwin thinks, in the 1840s and 50s, that the EoN is an essential part of evolution by natural selection. In particular, an ontic use of the EoN seems to ground his "wedges" metaphor, which describes the incessant drive of natural selection to change and improve organisms. As it appears in the *Origin,* it contains no mention of the EoN:

> The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force. (Darwin 1859, 67)

But the same passage in the *Sketch* makes it clear the structuring role that the EoN is to play here:

> If proof were wanted let any singular change of climate [occur] here … the pressure is always ready … a thousand wedges are being forced into the œconomy of nature. (Darwin 1909, 7–8)

The wedge metaphor, that is, only makes sense if the EoN – the "space" in which the wedges are packed, and which both determines their maximum number and provides the "forcing" that drives some out as others are pushed inward – is a preexisting feature of the environment, a set of affordances (or "places," in Darwin's terminology) which organisms are attempting to competitively exploit. In this early phase of Darwin's thought, we can be certain that less-fit forms will be ruthlessly exterminated only because of the ontic role played by the EoN. The Malthusian outpacing of available food supply by organismic growth, for example, is only a problem if the EoN exists prior to the outcomes of organismic struggle for resources. Darwin's use of the Malthusian model in the development of his own theory highlights his ontic use of the EoN – it constrains outcomes of organismic struggle by forcing organisms into a finite structure of 'places.'

While this seems to cement a role for both the ontic and explanatory roles of the EoN in Darwin's early thinking, several questions remain. For one, is Darwin's use of the EoN here static, or dynamic? The wedges metaphor does not seem to indicate one way or the other. And what are the facts that ground the ontic role of the EoN?

Begin with the first question. Darwin's clearest indication that the EoN is, for him, a dynamic concept, comes from a passage in the chapter of the *Sketch* on gradual appearance and disappearance of species. Here, Darwin writes that

> I need hardly observe that the slow and gradual appearance of new forms follows from our theory, for to form a new species, an old one must not only be plastic in its organization, becoming so probably from changes in the conditions of its existence, but a place in the natural economy of the district must ~~be made,~~ come

> to exist, for the selection of some new modification of its structure, better fitted to the surrounding conditions than are the other individuals of the same or other species. (Darwin 1909, 145, orig. deletion)

So important to Darwin was this insight that he footnotes this sentence to add, "Better begin with this."

The EoN, therefore, is not a static structure for Darwin. Places within it can come to exist and cease to exist, and this change within the EoN is not only an important process in the creation and destruction of species, but a prerequisite for natural selection to be able to construct a new species. Only if there is a novel affordance in the environment, currently unused by any organism, is it possible for a "better fitted" instance of evolutionary novelty to appear.

It is much more difficult, however, to determine just what facts in the natural world Darwin takes to ground the ontic role of the EoN as it is used here. This is made all the more difficult by the shifting nature of Darwin's use of the EoN. For the wedges metaphor, as already noted, has *lost* its reference to the EoN by the publication of the *Origin.* More than this, in Darwin's own copy of the first edition of the *Origin,* he strikes through the wedges passage (as noted by Francis Darwin in Darwin 1909, 8nn), and it disappears entirely in the second edition (Darwin 1860, 67).

To understand what happens to the EoN in Darwin after 1860, we must turn to the feature of Darwin's work that prior commentators, most notably Pearce (2009), have most strongly linked with the EoN: the principle of divergence. Kohn rightly notes a deep tension in this principle and its historical reception. On the one hand, Darwin himself, as he was busy writing the *Origin,* wrote in a letter to Hooker that "the 'principle of Divergence'…with 'Natural Selection' is the key-stone of my Book & I have very great confidence it is sound" (Darwin 1858), and it is arguable that one of the *Origin*'s largest impacts is, in Kohn's words, "the profound depth of ecological relationships and the very diversity of life that Darwin evoked through the principle" (Kohn 2009, 87). On the other hand, the principle of divergence was largely rejected and ignored by later authors in the history of biology. Ernst Mayr, for example, argues that it is "evident that Darwin failed to prove that the principle of divergence plays a primary role in speciation" (1992, 357).

What is the principle of divergence? Darwin is concerned at the end of the fourth chapter of the *Origin* with describing the manner in which the small amount of difference in character that separates varieties (a separation which all would have agreed could have been produced in nature) could "become augmented into the greater difference between species" (Darwin 1859, 111). The answer, Darwin says, is that while mere varieties will continue to compete with their parent species for the same food, resources, space, and so on, in nature, "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the *polity of nature,* and so be enabled to increase in numbers" (Darwin 1859, 112, emph. added).[13] Here, as with the wedges metaphor for natural selection, we see a clear invocation of the explanatory role of the EoN – diversification in natural populations is explained by the diversity of available places in the EoN. If there happen to be any unoccupied places in

[13] Unlike Linnaeus, Darwin uses the concepts of the "economy" and the "polity" of nature interchangeably.

a given area, Darwin argues, the filling of these places is advantageous to those organisms that are able to diversify enough to fill them. This, in turn, produces a selective pressure (think again of the wedges metaphor), driving organisms to diversify enough to occupy these new places.

We are not the first to argue for the claim that the EoN plays an explanatory role underlying Darwin's principle of divergence – Pearce (2009) makes the same case. We argue, however, that Pearce doesn't go far enough. This explanatory role not only allows us to infer the structure of the EoN from observations of natural populations (the same kind of structural explanation permitted, say, in McMullin's cases of genes or chemical elements), but the addition of the *ontic* role for the EoN allows us to license analogical inferences from this reasoning – using the putative structure of the EoN to make inferences about divergence and organismic distribution in a variety of similar contexts. That is, there is a two-way connection between the structural role of the EoN and the rest of Darwin's theory, making this structure an essential element of Darwin's work.

To draw from one of many examples, when he considers the evidence for the principle of divergence, Darwin moves from a claim about the environmental relationships underlying the EoN to a broader claim about diversification of structure:

> The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances. In an extremely small area, especially if freely open to immigration, and where the contest between individual and individual must be severe, we always find great diversity in its inhabitants. (Darwin 1859, 114)

The principle of divergence, then, offers us a way to make inferences about the nature and distribution of life, by extending our inferences about the EoN. We can also see these sorts of inferences at work in other places in the *Origin* where Darwin relies extensively on the principle of divergence. When discussing the role of isolation in generating species, Darwin frames the problem in terms of places in the EoN:

> [I]solation probably acts more efficiently in checking the immigration of better adapted organisms, after any physical change, such as of climate or elevation of the land, &c.; and thus new places in the natural economy of the country are left open for the old inhabitants to struggle for, and become adapted to…. (Darwin 1859, 104)

Physical change, that is, opens places in the EoN. Without isolation, those places might be filled by migration, but with isolation, they remain unfilled, ready to provide an advantage to organisms adapted to fill them by natural selection. Here again, we see the ability of the EoN to ground extended inferences about the causal processes that would lead to organisms' becoming better adapted to their environments. We may make inferences, for example, about increased adaptation and specialization on isolated islands on the basis of the structure of the EoN. But we may also use the adaptive trajectories of organisms on such islands to make claims about the nature of the places in the EoN. A similar claim can be made in the absence of isolation:

> Throughout a great and open area, not only will there be a better chance of favourable variations arising…but the conditions of life are infinitely

> complex from the large number of already existing species…. Each new form…will thus come into competition with many others. Hence more new places will be formed [in the EoN], and the competition to fill them will be more severe…. (Darwin 1859, 105)

Here, we can infer that whenever there is massive competition between organisms, that competition itself will open up places in the EoN (presumably, by subdividing previously extant places), while the smaller subdivisions and more complex nature of the local structure of the EoN in turn engenders fierce competition for the places as they now exist.

How should we understand this use of the EoN in the principle of divergence? First, it is worth noting that the rush of some authors to reduce the principle of divergence to nothing more than a specialized invocation of natural selection is ill-founded (unsurprisingly, one of the guilty parties here is Mayr 1992). That is, the principle of divergence is at least supposed to be a special sort of selection pressure, one which invokes the EoN in an unusual way – and it may even be intended by Darwin to be an influence on organisms different *in kind* from other, more traditional instances of natural selection. This basic underlying structure which the EoN (and related metaphors like the division of labor) is intended to describe does substantive work for Darwin, and we therefore take it that the explanatory role of the EoN, as evidenced both in the wedges metaphor and the principle of divergence (from Darwin's early and late work, respectively), is well established. It is unclear whether Darwin fully appreciated the role that the EoN was playing in his use of the principle of divergence. As we have shown, however, the explanatory use of the EoN is nonetheless clear.

We have persistently left open, however, the question of the status of the ontic role of the EoN for Darwin, and what facts in nature might ground that ontic role. It certainly seems as though Darwin is making use of the ontic role for the EoN. Our analysis of the wedges metaphor above relies on that ontic role, and the use of analogical extension of inference throughout Darwin's invocations of the principle of divergence also seems to indicate an ontic role. But is the existence of this structure just a brute fact for Darwin? Or is it grounded in further facts about the natural world? Here, Darwin is simply unclear, and it is likely that the question is not one that he ever considered. The best candidate for a set of grounding facts for the EoN is claims about the structure of the environment. But insofar as these are in part formed by organisms themselves, which are in turn governed by the EoN, it is not clear that Darwin could have constructed a consistent view of the EoN on this basis. As with the epistemic role above, it is also by no means certain that Darwin *intended* to invoke the EoN so as to give it an ontic role. It may be that apparent invocations of such a use are merely accidental on Darwin's part, and he had meant only to utilize the EoN in its explanatory role. The relationship between the explanatory and ontic roles in Darwin's thought must, it seems, remain unclear.

Before continuing, we should pause to set aside a question that will no doubt have occurred to those familiar with Darwin studies. The question of the EoN, especially insofar as it is tied up with Darwin's reading of Malthus, has formed a significant chapter of the extensive argument over Darwin's relationship to Victorian political economy (Gale 1972; Radick 2009; Hodge 2009a; Priest 2017). There are, however, several problems with the often-repeated claim that Darwin's invocations of the principle of divergence and the EoN are to be completely, or even primarily, explained by his relationship to Victorian proto-economics, particularly the work of Adam Smith (see, e.g., Kohn 2009). For one thing, Darwin never read, as far as we know, Smith's *Wealth of Nations* (though he did read Smith's *Moral Sentiments* and Dugald Stewart's memoir on Smith; Darwin 1859, 13r; Priest 2017, 578). It is thus not clear that he had any significant exposure to works of contemporary capitalist thought. Priest persuasively argues that Darwin's invocations of both the EoN and the "division of labor" are most likely to derive from sources like "Linnaeus, his grandfather [Erasmus Darwin], Humboldt, Lyell, and…other naturalists" such as de Candolle, not economists (Priest 2017, 579). Even if he had known the economic work well, however, it is not obvious, as Hodge has quite persuasively argued, that the industrial-capitalist context into which this story often places Darwin is really appropriate for his social circle. His family, particularly the Darwins, but also the Wedgwoods, primarily built their fortune through farming and land-holding, and Charles Darwin himself moved even farther away from the industrial world of Manchester, combining left-wing politics with trading in London stock options. Better, therefore, to connect him to the agrarian land-owner economy than to industrialized entrepreneurship (Hodge 2009a). Finally (and most importantly), the fairly direct line of transmission of the EoN from Linnaeus to Darwin should indicate clearly that, if anything, the proper economic sources to search for the roots of Darwin's use of the EoN are Swedish, and arise a century earlier, rather than those of nineteenth-century Britain. For all these reasons, we will pass over the question of Victorian British political economy in silence.

While it lacks the theological grounding of Linnaeus's EoN, then, the EoN plays an undeniable explanatory role for Darwin. Evolution by natural selection, in turn, is defined in intimate dialogue with this underlying structure, with phenomena in nature providing evidence for it and, in turn, being structured by it.[14] Darwin can accurately describe the principle of divergence as the "key-stone" of his work not because it is necessarily more important than natural selection or common descent (the two elements now most often recognized as the central claims of the *Origin*), but because it describes, at a single stroke, this complex relationship between the fact of common descent, the process of natural selection, and the EoN which both informs and is informed by the evolution of life. While the question of the ontic role for Darwin is much more fraught, we have offered some evidence that his arguments invoke the EoN in this way, even if it is difficult to discern what he took to ground this structure.

4 Moving forward: The modern synthesis and beyond

Use of the concept of the EoN most certainly changes in the period between Darwin's death and the rise of the Modern Synthesis. Less than a century after its extensive usage by Darwin, the EoN vanishes. Synthesis authors, such as Fisher, Wright, Mayr, and Haldane, almost never make reference to the EoN – Fisher, for instance, seems to use it only in three places, all before 1930. And this holds true throughout the life sciences by the middle of the twentieth century. In the entire print run of the journal *Nature*

[14] No teleological reading is meant by the use of "structured" here – we do not, for example, claim that this structure somehow directly *causes* organic change in nature to move in particular directions or paths.

(beginning in 1869), while the "economy of nature" is mentioned in 0.7% of articles in 1874, its usage falls off linearly over the next five decades, and after around 1930, it appears to be mentioned only in historical contexts.[15]

Given the extensive use of the EoN in structural explanations from Linnaeus to Darwin, an obvious question is therefore raised: what fills, at the very least, the explanatory role of the EoN as reference to it tails off through the beginning of the twentieth century? Do these structural explanations entirely disappear from biological theory over this time period, or is the explanatory role of the EoN taken over by something new? In the first few decades of the Modern Synthesis, we claim that there is a strong case to be made that much of the burden of the explanatory role was shifted to structures arising in genetics (emblematic, perhaps, of the neglect of ecology that some commentators have remarked upon during the Synthesis period; see Pigliucci 2007). As the explanatory role formerly played by the EoN is occupied by genetics, the apparent need for the entire concept disappears.

Evidence of this shift is sparse, but can be teased out in some of the relevant writings. Ernst Mayr, writing on the history of the biological species concept, notes that "the true role of the environment in evolution could not be understood until the nature of small mutations and of selection were fully comprehended" (1966, 3). The environment, far from offering places in the EoN and a structure against which evolutionary change should be understood (as Darwin would have seen it), is to be understood only in terms of selection, which is, in turn, driven genetically, by the accumulation of small mutations. A similar signal can be seen in Morrison's adept analysis of the debate between Fisher and Pearson over the nature of biological populations. For Pearson, she argues, as for Darwin, a population was "an integrated system," in which one must take account of preferential mating, "selection and environmental effects, all of which needed to be treated separately if one was to determine the genetic basis of the inheritance of particular characteristics" (Morrison 2002, 61). Fisher, on the other hand, assumes an indefinite number of Mendelian characters, an assumption unrealistic in natural populations. Taking Fisher as representative of the "future" of evolutionary theory, we have here, we claim, some indication of the explanatory role formerly carried by the EoN being instead served by a structure of small mutations in Mendelian characters, in some cases even abstracted away from real-world organisms.

For a slightly more detailed example, consider Sewall Wright's classic paper on shifting balance theory (Wright 1932). Wright begins by defining a background structure for evolutionary theory – here, again, not an ecological background, but a genetic background.

> Estimates of the total number of genes in the cells of higher organisms range from 1000 up. […] However, not all of this field [of possible gene combinations] is easily available in an interbreeding population. […] The population is thus confined to an infinitesimal portion of possible gene combinations, yet this

[15] This makes "economy of nature," even at its peak, around tenfold less common in *Nature* than "natural selection." This analysis was performed using the evoText website (Ramsey and Pence 2016), http://www.evotext.org. The data from this analysis are publicly available at https://doi.org/10.6084/m9.figshare.3189625.

> portion includes some 10^{40} homozygous combinations, on the above extremely conservative basis…. (Wright 1932, 356)

In Wright's case, the structure we must ensure in order to make evolution possible is not one of ecological places in the EoN, but of combinations of genes, and the position of the population lies not in ecological space, but in genotypic space, the space in which Wright's famous fitness landscapes are drawn. [16] In turn, just as we saw that, for Darwin, the preexistence of a place in the EoN is necessary for adaptive natural selection to occur, it is now characteristics of the adaptive landscape, defined genetically, that must be guaranteed. An extended quote makes the structural role played by genetics here clearest:

> The chance that a random combination is as adaptive as those characteristic of the species may be as low as 10^{-100} and still leave room for 10^{800} separate peaks, each surrounded by 10^{100} more or less similar combinations. In a rugged field of this character, selection will carry the species to the nearest peak, but there may be innumerable other peaks which are higher but which are separated by "valleys." The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field. (Wright 1932, 358–59)

The central question for evolutionary theory, Wright argues, is how populations manage to navigate rugged adaptive landscapes. Again, the basic structure here has now been completely abstracted from its ecological context; we have only innumerable combinations of genes into genotypes to track for the task of resolving the central questions of evolution. This is not, of course, to say that Wright was uninterested in environmental change, or the relationship between organisms and their environments (far from it; see an illuminating discussion in Hodge 2011). But environmental change, at least in the context of the 1932 paper, affects evolution primarily through its impact on the fitness landscape.[17] He writes that "[t]he environment, living and non-living, of any species is actually in continual change. In terms of our diagram this means that certain of the high places are gradually being depressed and certain of the low places are becoming higher" (Wright 1932, 362).[18] Again, we argue, we see an instance of the explanatory role for the EoN – as the background against which natural selection must be read as taking place – being occupied by the structure of genotypes, mutations, and their corresponding fitnesses.

[16] This view still holds currency today. Godfrey-Smith, for example, argues that one of the modes of action of natural selection is to "make a combination of traits more likely to appear by changing the array of backgrounds against which mutations arise," and considers the "absolute number of appropriate 'slots'" in which the occurrence of a mutation might produce a complex feature (Godfrey-Smith 2009, 50).

[17] This is also interestingly complicated by some of Wright's later work on the desert plant *Linanthus*, for instance (see Ishida 2017). While Wright takes this work as a broad confirmation of his Shifting Balance Theory, there is an emergent emphasis on the role of geographical distribution in population dynamics, which takes him a step or two closer to the genetic ecologists of the time. Even so, selection and drift occupy center stage throughout his work.

[18] Compare, for example, Pearce's claim that "as Lyell believed that changing physical and biological circumstances could affect the stations of animals, Darwin believed that these same changes could create new places in the economy of nature" (Pearce 2009, 518).

Two points are important to make here. First, we do not mean to argue that genetics is somehow a defective version of the structure rightly expressed by the EoN – no such normative conclusion is intended. Rather, we argue that this sheds interesting light on a heretofore neglected aspect (perhaps, even, a necessary precondition) of the shift from Darwinian biology to the biology of the early Synthesis. The rejection of the central role of the EoN allowed the Synthesis biologists to reframe problems that would normally have been solvable only in specific cases, requiring data about particular ecological scenarios, as general ones, requiring only (or only primarily) information about the structure of the relevant systems of heredity (think, here, of Wright's adaptive landscapes). The change in this fundamental structure underlying natural selection deserves significantly more attention from philosophers and historians of biology.

Secondly, the early Synthesis authors' quick replacement of the EoN by a structure arising from genetics should not be taken as evidence that there were no other significant invocations of structural explanation in the time between the 1920s and today. Nor, relatedly, do we want to claim that, even within the narrow field of genetics, all structural explanations were used as replacements for the EoN. To take only a few of the most significant examples, we have already mentioned McMullin's claim that 'gene' is a prime candidate for structural explanation. While we have been forced by considerations of space to ignore the history of ecology here (see footnote 10), it is also quite likely that the development of the concept of 'niche,' as well as population modeling efforts in ecology and mathematical biology more generally over the second half of the twentieth century, will involve structural explanation. These stories, as we will discuss below, are among those that we hope to see explored in future work.

5 Conclusions

We have argued that the EoN constitutes an invocation of structure which is interesting for a variety of reasons. Most importantly, as we have shown, while the structural explanations in which the EoN features continue to play a vital purpose – and point to an explanatory role for structure in the life sciences over a range of theories as varied as Linnaean classification and population genetics – the relationship between the ontic and explanatory roles of that structure is highly unstable over that same time period. In the work of Linnaeus, the EoN has clear ontic import. For Darwin, while he seems to utilize the EoN as though it played the ontic role, it is unclear what facts in the world would ground its ability to do so. And for biologists in the Modern Synthesis, the ontic role is jettisoned entirely, as a reductionist approach to the EoN gives it nothing more than a thin explanatory use, in turn to be explained away in terms of genetics.

What broader inferences can we draw from this example? While we hesitate to overgeneralize, here are a few points worthy of note. First of all, a McMullin-style realism, which makes inferences directly from the success of the explanatory role to belief in the ontic role, must be very careful in limiting its scope. There seems to be little evidence that the explanatory role of the EoN was unsuccessful at any point from Linnaeus forward, and yet the practicing scientists at issue varied wildly on their commitment to the EoN's ontic role, eventually providing for its replacement by a different set of grounding facts. Of course, McMullin is forthright in asserting that his version of realism "does not look at *all* science, nor at all future science, just at a good deal of past science which (let me say it again) might not have worked out to support realism the way it did" (McMullin 1984, 34). But the case examined here suggests that there is much more to be said about the relationship between the ontic and explanatory roles, and the sense in which the success of the latter might raise credence in the former.

Unlike McMullin's form of realism, OSR does hold ambitions to being a general picture of the relationship between scientific theories and the world, and recent work in that tradition has endeavored to expand its focus from its initial home in the physical sciences (French 2011). While we discussed the role of mathematical models in population genetics and ecology briefly above, it is worth seeing what lessons our case more broadly might have for practitioners of OSR. One of French's motivations in moving toward OSR is a concern about the ontological status of objects in the sciences at issue – if the foundations of quantum mechanics appear to undermine the ontological status of individual quantum particles as objects, then we should take such scientific deliverances seriously and construct an ontology which does not require commitment to such objects. While the more serious worries at issue in quantum mechanics (such as the outright failure of the individuality of particles) do not find parallels in the life sciences, French rightly notes that identifying biological individuals is no simple task (see, e.g., Bouchard and Huneman 2013).[19]

While structural relationships pointed out by the economy of nature are not likely to be of help in isolating particular biological individuals, one role they seem to play for Darwin is in differentiating *species* – recall his requirement that a place in the EoN open in order for a new species to be created. The idea of using the EoN as a way in which to distinguish species is a recessive one in the philosophy of biology, but the *ecological species concept* which it gives rise to is by no means unheard of (Van Valen 1976), and might well give a proponent of OSR a structural ontology for species.[20] If, on the other hand, this approach fails, then we have a place where a widely used structural explanation in the life sciences does *not* provide us with license to clearly infer anything about the ontological character of that structure. One might, at first blush, take this to be an argument against OSR. A rejoinder remains open to the OSR theorist, however – to respond that this invocation of structure, unlike those in other areas of the sciences, does not, in fact, ground ontological inference. To do this consistently, however, would require an account (not to our knowledge yet provided in the OSR community) that details which kinds of structural explanation ground ontological inference and which do not, which we believe would be a welcome addition to the OSR literature.

Finally, one overarching moral that we hope can be drawn here is that, just as the history of the physical sciences has been very fruitfully mined for discussions of structural explanation and structural ontology (discussion of Fresnel, Maxwell, Poincaré, and Einstein inaugurated contemporary structural realism; see Worrall 1989), so there is fertile work to be done in the history of the life sciences. As we have seen, the precise metaphysical commitments of the biologists we have discussed here can be exceedingly difficult to pin down in detail. But their approaches to

[19] Though this is by no means the only problem afoot in biological ontology – boundaries of individuals, populations, species, genes, and more all come under some degree of debate.

[20] To do so successfully would require the resolution of the potential circularity in the grounding of the EoN that we raised for Darwin, a task that we cannot pursue here.

theorizing were rich and sophisticated, and we hope that careful consideration of their use of concepts such as the economy of nature will enhance the broader conversation surrounding structure in the biological sciences and beyond.

Acknowledgments Many thanks to two anonymous reviewers for this journal, whose comments were extensive, charitable, and made the paper substantially better. Thanks to Trevor Pearce, Betty Smocovitis, and Michael Weisberg for comments on a previous version of this paper. Finally, thanks to an audience at the Centre for Logic and Analytic Philosophy Seminar at KU Leuven, especially Hugh Desmond, Jan Heylen, and Grant Ramsey; an audience at the History of Science and Contemporary Scientific Realism conference, especially Anjan Chakravartty, Mark Fuller, Stuart Glennan, Ioan Muntean, and Aaron Novick; and an audience at the Louisiana State University Philosophy Salon, especially Bradley Wood, William Eberhard, and Dolores Cowie.

References

Bokulich, A. (2016). Fiction as a vehicle for truth: Moving beyond the ontic conception. *The Monist, 99*(3), 260–279. https://doi.org/10.1093/monist/onw004.

Bouchard, F., & Huneman, P. (Eds.). (2013). *From groups to individuals: Evolution and emerging individuality*. Cambridge: The MIT Press.

Darwin, C. (1838a). "*Books to Be Read*" *and* "*Books Read*" *Notebook (1838–1851). CUL-DAR119*. Edited by Kees Rookmaker. URL: http://darwin-online.org.uk/: Darwin Online.

Darwin, C. (1838b). *Notebook E: [Transmutation of Species (10.1838–7.1839)]. CUL-DAR124*. Edited by Kees Rookmaker. URL: http://darwin-online.org.uk/: Darwin Online.

Darwin, C. (1838c). *Notebook N: [Metaphysics and Expression (1838–1839)]. CUL-DAR126*. Edited by Kees Rookmaker. URL: http://darwin-online.org.uk/: Darwin Online.

Darwin, C. (1858). Letter to J. D. Hooker. "Letter 2282 – Darwin, C. R. to Hooker, J. D., 8 [Jun. 1858]," June 8. https://www.darwinproject.ac.uk/letter/entry-2282.

Darwin, C. (1859). *On the origin of species*. 1st ed. London: John Murray.

Darwin, C. (1860). *On the origin of species*. 2nd ed. London: John Murray.

Darwin, C. (1909). *The Foundations of the Origin of Species: Two Essays Written in 1842 and 1844*. Edited by Francis Darwin. Cambridge: Cambridge University Press.

van Fraassen, B. C. (2006). Structure: Its shadow and substance. *British Journal for the Philosophy of Science, 57*(2), 275–307. https://doi.org/10.1093/bjps/axl002.

French, S. (2010). The interdependence of structure, objects and dependence. *Synthese, 175*(S1), 89–109. https://doi.org/10.1007/s11229-010-9734-2.

French, S. (2011). Shifting to structures in physics and biology: A prophylactic for promiscuous realism. *Studies in History and Philosophy of Biological and Biomedical Sciences, 42*(2), 164–173. https://doi.org/10.1016/j.shpsc.2010.11.023.

French, S. (2014). *The structure of the world: Metaphysics and representation*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199684847.001.0001.

French, S., & McKenzie, K. (2012). Thinking outside the toolbox: Towards a more productive engagement between metaphysics and philosophy of physics. *European Journal of Analytic Philosophy, 8*(1), 42–59.

Gale, B. G. (1972). Darwin and the concept of a struggle for existence: A study in the Extrascientific origins of scientific ideas. *Isis, 63*(3), 321–344. https://doi.org/10.1086/350940.

Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199552047.001.0001.

Hodge, M. J. S. (2009a). Capitalist contexts for Darwinian theory: Land, finance, industry and empire. *Journal of the History of Biology, 42*(3), 399–416. https://doi.org/10.1007/s10739-009-9187-y.

Hodge, M. J. S. (2009b). The notebook Programmes and projects of Darwin's London years. In M. J. S. Hodge & G. Radick (Eds.), *The Cambridge companion to Darwin* (2nd ed., pp. 44–72). Cambridge: Cambridge University Press. https://doi.org/10.1017/CCOL9780521884754.003.

Hodge, M. J. S. (2011). Darwinism after Mendelism: The case of Sewall Wright's intellectual synthesis in his shifting balance theory of evolution (1931). *Studies in History and Philosophy of Biological and Biomedical Sciences, 42*(1), 30–39. https://doi.org/10.1016/j.shpsc.2010.11.008.

Ishida, Y. (2017). Sewall Wright, shifting balance theory, and the hardening of the modern synthesis. *Studies in History and Philosophy of Biological and Biomedical Sciences, 61*, 1–10. https://doi.org/10.1016/j.shpsc.2016.11.001.

Jackson, M. W. (1994). Natural and artificial budgets: Accounting for Goethe's economy of nature. *Science in Context, 7*(3), 409–431. https://doi.org/10.1017/S0269889700001769.

Koerner, L. (1999). *Linnaeus: Nature and nation*. Cambridge: Harvard University Press.

Kohn, D. (2009). Darwin's keystone: The principle of divergence. In M. Ruse & R. J. Richards (Eds.), *The Cambridge Companion to the "Origin of Species,"* (pp. 87–108). Cambridge: Cambridge University Press.

Ladyman, J. (1998). What is structural realism? *Studies in History and Philosophy of Science, 29*(3), 409–424. https://doi.org/10.1016/S0039-3681(98)80129-5.

Ladyman, J., & Ross, D. (2007). *Every thing must go: Metaphysics naturalized*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199276196.001.0001.

Linnaeus, C. (1762). *Miscellaneous Tracts Relating to Natural History, Husbandry, and Physick*. Edited by Benjamin Stillingfleet. 2nd ed. London: R. and J. Dodsley.

Linnaeus, C. (1763). "Skaparens afsikt med naturens verk. En promotionsföreläsning af Linné." Edited and translated by Arvid Hj. Uggla. *SLÅ* XXX (1947), 71–96.

Linnaeus, C. (1781). In F. J. Brand (Ed.), *Select dissertations from the Amoenitates Academicae* (Vol. 1). London: G. Robinson.

Mayr, E. (1966). *Animal species and evolution*. Belknap: Cambridge.

Mayr, E. (1992). Darwin's principle of divergence. *Journal of the History of Biology, 25*(3), 343–359. https://doi.org/10.1007/BF00351996.

McMullin, E. (1984). A case for scientific realism. In J. Leplin (Ed.), *Scientific Realism* (pp. 8–40). Berkeley: University of California Press.

Morrison, M. (2002). Modelling populations: Pearson and Fisher on Mendelism and biometry. *British Journal for the Philosophy of Science, 53*(1), 39–68. https://doi.org/10.1093/bjps/53.1.39.

Morrison, M. (2014). Fictional models in science. *Physics World, 27*(2), 29–32. https://doi.org/10.1088/2058-7058/27/02/39.

Ospovat, D. (1981). *The development of Darwin's theory: Natural history, natural theology, and natural selection* (pp. 1838–1859). Cambridge: Cambridge University Press.

Pearce, T. (2009). 'A great complication of circumstances' – Darwin and the economy of nature. *Journal of the History of Biology, 43*(3), 493–528. https://doi.org/10.1007/s10739-009-9205-0.

Pigliucci, M. (2007). Do we need an extended evolutionary synthesis? *Evolution, 61*(12), 2743–2749. https://doi.org/10.1111/j.1558-5646.2007.00246.x.

Priest, G. (2017). Charles Darwin's theory of moral sentiments: What Darwin's ethics really owes to Adam smith. *Journal of the History of Ideas, 78*(4), 571–593. https://doi.org/10.1353/jhi.2017.0032.

Radick, G. (2009). Is the theory of natural selection independent of its history? In J. Hodge & G. Radick (Eds.), *The Cambridge Companion to Darwin* (2nd ed., pp. 147–172). Cambridge: Cambridge University Press.

Ramsey, G., & Pence, C. H. (2016). evoText: A new tool for analyzing the biological sciences. *Studies in History and Philosophy of Biological and Biomedical Sciences, 57*, 83–87. https://doi.org/10.1016/j.shpsc.2016.04.003.

Rausing, L. (2003). Underwriting the Oeconomy: Linnaeus on nature and mind. *History of Political Economy, 35*(5), 173–203. https://doi.org/10.1215/00182702-35-Suppl_1-173.

Reill, P. H. (2005). *Vitalizing nature in the enlightenment*. Berkeley: University of California Press.

Richards, R. J. (2002). *The romantic conception of life: Science and philosophy in the age of Goethe*. Chicago: University of Chicago Press. https://doi.org/10.7208/chicago/9780226712185.001.0001.

Rohwer, Y., & Rice, C. (2016). How are models and explanations related? *Erkenntnis, 81*(5), 1127–1148. https://doi.org/10.1007/s10670-015-9788-0.

Ruse, M. (2009). The origin of the *Origin*. In M. Ruse & R. J. Richards (Eds.), *The Cambridge Companion to the "Origin of Species,"* (pp. 1–13). Cambridge: Cambridge University Press.

Schabas, M. (2003). Adam Smith's debts to nature. *History of Political Economy, 35*(5), 262–281. https://doi.org/10.1215/00182702-35-Suppl_1-262.

Schabas, M. (2005). *The natural origins of economics*. Chicago: University of Chicago Press. https://doi.org/10.7208/chicago/9780226735719.001.0001.

Stauffer, R. C. (1960). Ecology in the long manuscript version of Darwin's 'Origin of Species' and Linnaeus' "Oeconomy of Nature". *Proceedings of the American Philosophical Society, 104*(2), 235–241.

Van Valen, L. (1976). Ecological species, multispecies, and oaks. *Taxon, 25*(2/3), 233. https://doi.org/10.2307/1219444.

Wilkins, J. S. (2009). *Species: A history of the idea*. Berkeley: University of California Press.
Worrall, J. (1989). Structural realism: The best of both worlds? *Dialectica, 43*(1–2), 99–124. https://doi.org/10.1111/j.1746-8361.1989.tb00933.x.
Worster, D. (1977). *Nature's economy: The roots of ecology*. San Francisco: Sierra Club Books.
Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth International Congress of Genetics, 1*, 356–366.