The Economy of Nature: The Structure of Evolution in Linnaeus, Darwin, and Toward the Extended Synthesis

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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, its reconceptualization in genetic terms during the Modern Synthesis, and concluding with the prospects for its reunion with broader ecological themes in a potential, future Extended Synthesis. This structural element has thus been preserved across changes between theories radically different in their ontological, methodological and philosophical commitments, and offers us an exciting focal point for investigating the development of biological theory over the last three centuries.

Keywords: economy of nature; Carl Linnaeus; Charles Darwin; Sewall Wright; Ernst Mayr; extended synthesis; ecology; eco-evo-devo

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.* Structure has proven to be a valuable way to approach the interpretation of quantum field theory (French and McKenzie 2012), and structural realism, whether in its original epistemic (Worrall 1989) or newer ontic form (Ladyman and Ross 2007; French 2010; French 2014), has reinvigorated the case for scientific realism more broadly.

This pursuit of structure, however, has broadly passed over the biological sciences. In one of the first articles to make reference to any sort of structural realism, Ernan McMullin makes a passing reference to the "elegant example" of the gene as a concept whose realist import should be cashed out structurally (McMullin 1984, 28), but beyond this possibility, which has not been developed, biology was left out of the shift to structures until quite recently.[1] In one rather straightforward sense, this is entirely explicable. Biology certainly lacks the kind of mathematical structure that one finds, for example, encoded in the algebraic structure (or one's favored alternative formalism) of quantum field theory (Halvorson 2007). Even in places where biology has been extensively "mathematized," such as population genetics (Provine 1971), theoretical population biology (Charlesworth 1980), or newer research traditions such as adaptive dynamics (Dercole and Rinaldi 2008), we still tend to have mathematical frameworks that are narrow in scope, circumspect in application, and not considered to be in any way "constitutive" of the behavior of the traits, organisms, or populations which they describe. The kind of structure that proponents of ontic structural realism (OSR) prefer, then, will be much more difficult to "read off" of the relevant biology.

We argue here, however, that there is still room to find structure in biology – but it will not look like the structures of the physical sciences. To do so, we turn our focus backward, considering what we claim is an underappreciated instance of theoretical continuity in the biological sciences. The concept

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

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 theory change. When we pursue it through the development of genetics and the Modern Synthesis, we find that while the explanation for what plays this structural role changes almost beyond recognition, the structural element nonetheless remains. What we have here, then – in line with McMullin's appeal to the long-term preservation of structures through theory change – is a structural feature that biologists have felt the need to account for across a wide variety of theories, vastly different in their other scientific, philosophical, and even theological assumptions. While this, of course, looks nothing like the appeal to structures made by proponents of OSR, we argue that it is indeed vital to our understanding of the shifting landscape of biological theories in the last two centuries.

In the second section, we begin by considering the works of Linnaeus, including the intellectual context which inspired them. Section three discusses the ways in which Darwin picks up on these themes in Linnaeus. The fourth section speculatively pushes these considerations into the period of early genetics and the Modern Synthesis, while the last section considers the relationship between our work here and recent efforts to agitate for a rethinking of biological theory, an "extended synthesis."

2. Linnaeus's Economy of Nature

Before diving into a proper analysis of Linnaeus's understanding of the economy of nature, we should begin by saying something about the economic and theological themes that ground his thinking. The histories of these themes, in turn, are deeper and richer than we can cover here, so this will constitute little more than a historical primer on the intellectual traditions that Linnaeus inherited. While clearly not exhaustive, we hope that the reader develops some appreciation of the landscape that helped to shape the work of Linnaeus (and so Darwin, through him).

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 notion of *structure* in the world, which we argue is crucial for understanding what's happening in the works of Linnaeus and Darwin alike. The influence of theology on biological work throughout the European continent is apparent even 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).[2] In the 1750s, Albrecht von Haller's theory 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, appealing to God in particular as 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 writer's 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

2 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.

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 notion has clear theological roots.

This commitment to the notion of a rationally structured world makes it easy to see why it would be 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).[3] 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 notion 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 the "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 that the world in general can be understood to

3 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.

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).[4] 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). Indeed, 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. His conceptions of nature's economic order and human economics mirror one another in the manner just described for others of his time. 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 economy of nature (hereafter 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

4 "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.

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 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.

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. This becomes even clearer when Linnaeus speaks in terms of the *Polity* of nature, best construed as analogous to the idea of "police" (Rausing 2003, 175).[5] This should not be confused with the notion of police that we might

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

glean from the contemporary use of the term. As Lisbet Koerner (1999, 82–3) makes clear, Linnaeus' conception of *policing* is tightly related to his broader conception of "divine economy."[6] 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's a clear sense in which the relations appear to be, analytically at least, prior to the relata. That is, the relational structure of the world is such that there really are particular "stations" in the world that certain actors are created to occupy. This fits quite comfortably with a picture of nature that's 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.[7] But, whatever the case theologically, Linnaeus sees the basic concept of the EoN as one with epistemic and ontological import. 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 concept itself continues to do work, as we shall see.

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6 Koerner cites (and quotes) a 1763 sermon delivered by Linnaeus, 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.

7 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.

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 1838a, 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 1838b, E 58).[8] 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 and the first preparation of the *Sketch* in 1842,[9] 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).

Darwin thinks, in the 1840s and 50s, that the EoN is required in order to understand natural

8 Completing the standard picture of selection in the *Origin,* Darwin adds the analogy with artificial selection the following week (Darwin 1838b, 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).

9 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.

selection. In particular, the EoN plays a pivotal role in his "wedges" metaphor, describing 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 against the background of the EoN. It is this structure which sets the "places" into which the wedges are aiming to be driven – the wedges will only fail to fit if this number of places is finite, and the way that Darwin speaks of the "driving" action of superfecundity and competition, both elements of natural selection, only makes sense when occurring within such a structure.

The clearest invocation of this dependence of natural selection on the EoN comes from a passage in the chapter of the *Sketch* on gradual appearance and disappearance of species. Here, Darwin argues 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."

This is not, however, the last word on the EoN in Darwin. For the wedges metaphor, as already noted, has *lost* its reference to the EoN by the publication of the *Origin.* In Darwin's own copy of the first edition of the *Origin,* he even 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 considerations of the EoN after this shift, we must turn to the feature of Darwin's work that prior commentators, most notably Trevor 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).[10] Once again, we see the EoN forming a background structure against which natural selection plays out. In this case, Darwin argues that if there should be unoccupied places in the EoN in a given area, the filling of these places forms a great advantage to those organisms

10 Unlike Linnaeus, Darwin uses the concepts of the "economy" and the "polity" of nature interchangeably.

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 should pause here 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). 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*; Darwin 1838a, 13r). Even if he had, 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. Better, it seems, to connect him to the agrarian land-owner economy than the entrepreneurship of Manchester (Hodge 2009a). Finally (and most importantly), the fairly direct line of transmission of this concept 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. For all these reasons, we will pass over the question of Victorian British political economy in silence.

We are not the first to argue for the claim that the EoN is a necessary background to Darwin's principle of divergence – Pearce (2009) makes the same case. We argue, however, that Pearce doesn't go far enough. For in addition to using the structure exemplified by the EoN to make inferences about the principle of divergence, Darwin further employs both the principle of divergence and the role of the EoN in natural selection to make inferences *about* the structure of nature itself. 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, the inference moves in this opposing direction:

> 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 what the structure of nature should be like in circumstances like those that Darwin describes here. We can also see these bidirectional 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 two-way utility of the EoN. We may make inferences, for example, about increased adaptation 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.

We argue, then, 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). This basic underlying structure which the EoN (and related metaphors like the division of labor) is intended to describe does substantive philosophical work for Darwin, more than simply giving a name to a special class of explanations already covered by natural selection. They serve as epistemic guides to a structure that Darwin claims to genuinely exist in the world.

While it lacks the theological grounding of Linnaeus's EoN, then, the role of the structure in the natural world which this term points out is largely the same for Darwin. Evolution by natural selection is defined in intimate dialogue with this underlying structure, with phenomena in nature providing evidence for it and, in turn, being structured by it.[11] 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 structure of nature which both informs and is informed by the evolution of life.

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

11 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.

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* (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.[12]

Given the vital structural role which we have argued the EoN played from Linnaeus to Darwin, an obvious question is therefore raised: what fills the role of the EoN as it tails off through the beginning of the twentieth century? Does the structure itself disappear from biological theory over this time period, or is it explained by something new? We claim that there is a strong case to be made that (as in so many other parts of evolutionary theory) much of the burden of this structural role was subsumed by the advancement of genetics (and, as some commentators have argued, the decline in the presence of ecology more generally in the Modern Synthesis; see Pigliucci 2007, and about which more later). As the structural 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 Synthesis-era 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

12 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 with doi:10.6084/m9.figshare.3189625.

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 shift in focus from the ecological framework implied by the EoN to a statistical, genetics-first picture of evolutionary theory.

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

Here, 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.[13] 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

13 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).

> 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 in order to have fully resolved 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. 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).[14] Again, we argue, we see an instance of a structural role – the background, against which natural selection must be read as taking place – being occupied not by the ecologically focused EoN, but rather by nothing more than genetics.

This is not to say 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 information about the structure of the relevant systems of heredity (think, here, of Wright's adaptive

14 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).

landscapes). The shift in this fundamental structure underlying natural selection deserves significantly more attention from philosophers and historians of biology.

5. Conclusions

Let's take stock. As developed and deployed at least by the time of Linnaeus, the idea of the economy of nature forms a structural element present in biology, and one that is preserved, at least in some form, through to the Modern Synthesis. The motivations and cultural contexts that inform the precise dimensions of these structural themes are diverse. We have argued, nonetheless, that something of the core character of the EoN as a concept is retained throughout the historical change outlined here.

What of the fate of the EoN in the years since the hardening of the Modern Synthesis? Recent work – primarily thanks to the advancement of evolutionary developmental biology – has shifted our focus toward the possibility of an "Extended Synthesis," one which reunites the population-genetic framework built in the middle of the twentieth century with insights from other fields, both those that had not yet been developed and those that had been set aside by the Modern Synthesis. Foremost among those in the discarded category is the study of development, where an integrative understanding of concepts such as constraint, canalization, and generative entrenchment stands ready to revolutionize our understanding of evolution (Griffiths and Gray 1994; Wimsatt 2001; Jablonka 2006; Callebaut, Müller, and Newman 2007). Evidence from microbial systems (Goldenfeld and Woese 2007), and from molecular biology more broadly (O'Malley et al. 2014), are opening new lines of research, and even our understanding of genetics itself may prove in need of an update (Lynch 2007; Stern and Orgogozo 2009).

As Pigliucci and Müller note, however, "curiously largely unnoticed is the fact that ecology also missed out on the Modern Synthesis" (Pigliucci and Müller 2010, 8). While a significant amount of recent interest has been paid to the role of niche construction as a mechanism of epigenetic inheritance

(Odling-Smee, Laland, and Feldman 2003; Schulz 2014), this interest has not yet, or at least not significantly, expanded to include broader questions in ecology (though recent discussion of "eco-evo-devo" may begin to close this gap; see Abouheif et al. 2014; Gilbert, Bosch, and Ledón-Rettig 2015). The relationship between ecology and the EoN is a question that will doubtless have already occurred to readers. Without taking a detour into the history of ecology and the transformations of the EoN concept which have undoubtedly occurred there (Worster 1977), it is clearly remarkable that the retreat of the EoN coincides with the development of ecology as an independent field.[15]

One reason for the growing recognition of the absence of ecology from the Modern Synthesis, we propose, is recognition of the failure of the genetic reconceptualization of the EoN to adequately capture what we now recognize to be the structure of the environment. Gilbert, Bosch, and Ledón-Rettig, for example, argue that "the environment is not merely a selective filter," as "developmental plasticity transforms the environment into an active agent in shaping the phenotype" (2015, 620). Contemporary evolutionary biology, Abouheif et al. argue, will have to "uncover the relationships within and among different levels of biological organization," where this includes not just the well known molecular-organismic divide, but "levels of organization external to the individual organism [which] extend to higher levels, such as groups, populations, and communities" (2014, 119). All of these goals are far too much to ask of the "space of potential gene combinations" offered by the Modern Synthesis, and hearken back to a richer, more detailed picture of the structure of the natural environment. And far from being a new development – or even a development as recent as the construction of ecology in the early twentieth century – we see here an attempt to reconnect with an understanding of the structure of the environment that dates back centuries.

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15 While the use of "economy of nature" tails off, as was discussed in the last section, around 1930, the journal *Ecology* was first published in 1920.

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