

1. Introduction

Abstract. This book is about claims that the Modern Synthesis requires an extension. In this chapter I outline the approach taken to inspecting this position and give a brief overview of the reasons some have come to argue for extension. In doing this I introduce core elements of the argument to come, including the distinction between theories of population and of form and the concept of information. Population level theories are those of Darwinism and the Modern Synthesis which distinctly removed transformational arguments of the sort associated with Lamarck. Information has been recruited by many theorists, but its use has been colloquial, and this has led to problematic interpretations. It is a plea for the proper use of information that is at the heart of this book and in this chapter I signal its importance. This chapter, and this book, do not exhaustively inspect all aspects of the argument for extension, but predominantly focus upon claims made from development. This choice has been made to demonstrate the kind of thinking at play on both sides of the debate.

Keywords. Conceptual ecology · Modern Synthesis · Extended Evolutionary Synthesis · Development · Population · Form · General Darwinian Theory · Special Theory of Evolution · Theoretical structure · Information

1.0 Scholasticism and conceptual ecology

Whilst writing this book I had a useful conversation with the psychologist Richard Bentall and my father, David Dickins, about other matters. During that conversation Bentall mentioned a theological difference between Christianity and Islam. He argued that the Islamic tradition regards the Koran as the given word of God; the Christian tradition sees the Bible as an interpretation of the word of God. By inference this means that Christian theologians and scholars have a theoretical job to do, whilst Islamic scholars have an educational mission.

This caused me to wonder whether advocates of particular scientific positions, paradigms and theories operate in one or both of those modes – the interpretive or the pedagogic. This book is about the Modern Synthesis in evolutionary biology and those who have, in recent years, sought to extend it. That use of the term *extend* is broad with some advocates of an extended thesis looking for minor changes to

what is seen as the standard theory of evolution, and others looking to completely replace it. Unlike Islam and Christianity there is no foundational text for the Modern Synthesis, but rather a collection of texts, that grew from interpretations of Darwin's *Origin* and the responses from scientists to it. This in turn led to a vast empirical and theoretical literature exploring the hypothesis space that is associated with the Modern Synthesis. Empirical and theoretical work necessarily makes an interpretation, but quite often that interpretation is a declarative statement along the lines that *the Modern Synthesis causes us to think x, here are some entailments of x empirically or theoretically endowed*.

There is also a meta-literature within the history and philosophy of science, which I see as a discipline positioned on a continuum between pure historians and pure philosophers. In the middle are those who use historical example to draw out philosophical points, which runs the risk of sampling error and should not be treated inductively, but can be enormously revealing about the array of thoughts possible within a scientific realm. These scholars also act to interpret the words of evolutionary biologists, and to make sense of the Modern Synthesis.

All of the preceding scholars, then, are interpretive and also exploratory. Whilst the scientific response is perhaps a more direct interaction with, and interpretation of Nature, the meta-literature is informed by science and in turn informs scientists, helping them to consider and adjust their own view. Moreover, there are scholars who operate at the direct and meta-levels. All, then, share the project of interpreting Nature at varying degrees of separation.

This interpretive space is dynamic, as new findings and new ideas continue to enter. It would be strange to find the interpretations and journeys of all scholars in perfect alignment with one another. As they diverge, we should expect some to note their parting of ways with particular positions and thinkers, and to make clear the distance between them and the directions they are individually taking. A key question in the current debates about the Modern Synthesis is whether or not all of the scholars addressed to its interpretation are roaming the same land. If they are, then perhaps they are mapping new regions, and occasionally advocating additions to current global descriptions. This might be equivalent to crossing England from West to East. If your life had been lived only in the county of Devon your general model of England would currently be one of extensive dairy pasture and the depauperate ecology that sustains. A trip to the county of Essex will expose you to vast deserts of cereal crops and a different, but not completely different ecology¹. One should not be an essentialist about England, but that area which we choose to call England varies in discernible ways and one can map ecological gradients across it. This journey would impose a certain generality on the account of our Devonian ecologist.

¹ For example, the Devonian would be surprised to find some, but not enough, Yellowhammers (*Emberiza citrinella*) in Essex that hang on due to available winter seed and some remnant hedgerow for nesting (Bradbury & Stoate, 2000).

Continuing the metaphor of the theoretician as ecologist, mapping a space of possibilities, we might think of another Devonian who had never travelled. Her data on diversity and abundance will be mapped over time and she will have a phenomenally detailed account of Devon in terms of its flora, fauna and their interactions. She will be a specialist in that community, and the granularity of her accounts will be finer than those of her travelling colleague.

If we think of England as the whole of evolutionary biology, then we have a country made up of different counties. Each county would be a particular specialism, akin to population genetics, the study of speciation, paleobiology, and so on. And within each county traditions would develop to deliver those tasks, and the local management of ideas would take on a particular pattern that delivered local scientific understanding but also helped to make sense of the practices in neighbouring counties. But the further east one travelled from Devon the more stretched your local ecological model would become.

We can stop the metaphor at this point and draw some lessons. First, evolutionary biology, whilst about evolution as a kind of change, makes contact with the whole of biology as a discipline. There is great diversity in its offer. Conceptually that diversity is ever present, but ecologists had to discover it as they journeyed, much as our travelling Devonian discovered new communities on her way to Essex. Nature had to be interpreted. As she travelled, she would meet resident ecologists in each county and their specialisms would grade across the English landscape, but those from Hertfordshire would have greater interpretative difficulty when talking to those from Somerset, than would our Devonian. Nonetheless, the realization of all these ecologies is a wondrous thing and our itinerant ecologist will make great effort to bring these ideas together, to find a *lingua franca* in which they could all pose their questions, express their answers and move forward together, sharing their collective access to Nature. She will seek unity through interpretation.

In the beginning was the *Origin*, and the *Origin* asserted evolution as a fact but also gave a theory of it. That theory was immediately interpreted in different ways, leading to diversity of opinion. The Modern Synthesis was a period in which that diversity was directly addressed, and a common framework was developed in the spirit of unification. Those seeking extension, by way of minor modifications to the Modern Synthesis, are in many ways pursuing the same project. They understand the Modern Synthesis as a continuing journey, a constant effort to understand, and they simply look to extend our shared vocabulary. But those seeking to do away with the Modern Synthesis are perhaps those who have stayed firmly within a particular sub-discipline, landlocked in their county and developing bespoke accounts of their idiosyncratic niche. This has made communication difficult at the national level, and their solution is to start again and create a new *lingua franca*, based on their language, based on their direct access to Nature. This book focuses upon developmental theorists who, for whatever reason, have felt themselves isolated from the Modern Synthesis and in response have presented what they consider to be a different view of evolution. At times this work appears interpretive and at others it appears pedagogical.

1.1 A survey of the conceptual landscape

I regard the Modern Synthesis as two things. First, it is an extended period of activity within the field of evolutionary biology. This was the time in which evolutionary biology was established as a discipline in its own right. Second, the Modern Synthesis is a framework for setting questions and developing explanations. It is a theory, but in the grand sense of that term. It represents a way of thinking about biology and evolution that provides scientific understanding. But as a grand theory, or framework, it is not unspecialized or unfocused.

The Modern Synthesis is so called, thanks to Julian Huxley (Huxley, 2010), because of the resolution of debates between the Darwinian biometricians and the Mendelian mutationists (Chapters 2 and 3). That resolution was due to the work of early population geneticists who showed a way for particulate genes to engage in gradual Darwinian process. But the synthesis did not stop at this point, and much else was developed following these leaps in understanding in the 1900s. Indeed, the synthesis was a continued process of unification into the second half of the 20th century (Delisle, 2017; Mayr, 1982; Smocovitis, 1992, 1996) as we shall see in Chapter 3.

Aspects of the Modern Synthesis have received criticism. Criticism was integral to the process of the synthesis itself, but in the post synthesis period scientists did not have to wait long for theorists and biologists to start rethinking what the Modern Synthesis delivered and the wisdom of some of its theoretical directions (e.g. (Eldredge, 1971; Eldredge & Gould, 1972; Gould, 1982, 2002; Gould & Eldredge, 1977; Gould & Lewontin, 1979; Vrba & Gould, 1986)). Some of these discussions were about fine details of theory. For example, the discussions about punctuated equilibrium that were initiated in the 1970s by Eldredge and then Eldredge and Gould, were really only discussions about the role of allopatric speciation in evolution, that had already been had by Mayr (Mayr, 1989). As Mayr noted, the discussions of the 1970s had a tendency to gloss details, interpreting Darwinian gradualism as even in tempo, when in fact Darwin had taken pains to discuss different rates of evolution. But what is most interesting about Mayr's analysis of punctuated equilibrium is how carefully he unpicks all the claims, relates them to prior argument or findings, and points to problems that remain to be resolved. He is also clear to separate this discussion from saltationism, which was the idea of the spontaneous macromutations upheld by early Mendelians.

What Mayr's fastidiousness tells us is that there are debates to be had within the Modern Synthesis that are considered reasonable, and the framework gives the limits. Those limits are marked by topics that are regarded as either anathema to the Modern Synthetic way of thinking, or as having been resolved. Gould (2002) famously discussed these limits as having been established first through a process of restriction in which Lamarckism, saltationism, and orthogenesis were removed from evolutionary thinking. But as I have noted elsewhere with Ben Dickins, this restriction still permitted a good amount of pluralism in thought, and is perhaps

better associated with the neo-Darwinian period (Dickins & Dickins, 2018). Gould's second stage of the synthesis was one of a hardening, of a certain form of dogmatism taking hold that focused upon natural selection as the predominant source of evolutionary change. But as Dickins and Dickins show at least one leading text book of evolutionary biology lists the sources of evolutionary change as natural selection, gene flow and genetic drift (see (Futuyma, 1986; Ridley, 2004)).

1.1.1 Some comments on extending the synthesis

In the introduction to their edited book on the *Extended Evolutionary Synthesis*, Pigliucci and Müller tell us that the Modern Synthesis has defined evolutionary theory since the 1940s even in light of developments in methods and domains such as molecular genetics, developmental biology, and the various -omics (Pigliucci & Müller, 2010a). They tell us that they have collected leading experts to write under the title of an *Extended Synthesis* in order to display what they see as a “multifaceted research program” that is a “work-in-progress” (Pigliucci & Müller, 2010a: 3). This research program has emerged from these new developments.

Whenever we talk to colleagues who are inclined toward a conservative position about the status of evolutionary theory, we are confronted with the question “So, what exactly is so new that we may speak of an Extended Synthesis?” This volume is the beginning of a response to that question... The commonest reaction to our explanations is something along the lines of “But that is already understood as part of the Modern Synthesis anyway.” We beg to differ. Many of the empirical findings and ideas discussed in this volume are simply too recent and distinct from the framework of the MS to be reasonably attributed to it without falling into blatant anachronism. Concepts such as evolvability for instance, did not exist in the literature before the early 1990s; phenotypic plasticity was known, but consistently rejected as a source of nuisance, not of significant micro- and macro-evolutionary change. Or consider EvoDevo, an entirely new field of evolutionary research that has emerged in full only since the late 1980s, precisely because of the perceived explanatory deficits of the MS in the realm of phenotypic evolution. Yet another common retort to our arguments is that the new ideas are “not inconsistent” with the framework of the Modern Synthesis; this may very well be true – and most of us would gladly agree – but being consistent with the MS is not at all the same thing as being a part of the MS! (Pigliucci & Müller, 2010a: 4)

Pigliucci and Müller hypothesize that biologists may have simply upgraded their own understanding of evolutionary theory without reference to the distance travelled from the concepts in play during the formation of the Modern Synthesis; and indeed, many of them may never have had the time to do the historical work in their own field. The implication is that biologists are enculturated by the science they are taught and do, and the label of the Modern Synthesis has been applied without much thought to their own practices. Their own practices may well be entirely consistent and rational, but they are not necessarily those of the synthesis. What this means is that Pigliucci and Müller think that the Modern Synthesis represents a clear and

defined set of theoretical assumptions and ideas, and that those have been challenged by work since the 1940s.

After making these points Pigliucci and Müller move on to a sketch of the Modern Synthesis that covers ground I cover in more detail in Chapters 2 and 3. Indeed, I have written those chapters in order to present the kind of history of evolutionary thought that is most typically referred to by those advocating for an Extended Evolutionary Synthesis, drawing on the same literatures that they do. This helps me to place the arguments I deal with, but it does not mean that *this* history is a correct rendition of this long period in scientific development. It simply shows a set of possible interpretations and ideas. More importantly, it shows what the scholars involved in the ongoing arguments both for and against the Modern Synthesis are arguing about. In this case, Pigliucci and Müller tell us that key areas of biology were left out of the Modern Synthesis, including developmental biology and ecology: this is the claim for isolation, for being left within a county studying its local natural history. What was included in the synthesis they highlight by quoting Futuyma's text book in which he lists the key principles of the synthesis (Futuyma, 1986), given below as a bulleted list:

- Populations contain genetic variation
- Genetic variation arises at random via mutation and recombination, and is not directed toward adaptation
- Populations evolve by changes in gene frequency themselves caused by genetic drift, gene flow, and especially natural selection
- Adapted genetic variants have slight phenotypic effects making phenotypic change gradual (although there are some alleles with discrete effects that may be useful)
- Diversification is caused by speciation, normally caused by the gradual emergence of reproductive isolation among populations
- These micro-evolutionary processes above can, over long time, lead to macro-evolutionary change

This list sets the agenda for possible challenges, and indeed all these principles are expressed with a clarity that permits challenge. But Pigliucci and Müller clarify the kind of challenge their book contains, and they do this by giving what they consider to be a parallel example, that of the Central Dogma of Molecular Biology.

The dogma ... stated that the flow of information in biological systems is always one way, from DNA to RNA to proteins. Later on, however, it was discovered that the DNA>RNA flow can be reversed by the appropriately named process of reverse transcription, which takes place in a variety of organisms, including some viruses and eukaryotes (through retrotransposons). Moreover, we now know that some viruses replicate their RNA directly by means of RNA-dependent RNA polymerases, enzymes also found in eukaryotes, where they mediate RNA silencing. Prions have shown us how some proteins can catalyze conformational changes in similar proteins, a phenomenon that is not a case of replication, but certainly qualifies as information transfer. Finally, we also have examples of direct DNA translation to protein in cell-free experimental systems in the presence of ribosomes but not of mRNA. All of these molecular processes clearly demolish the alleged central

dogma, and yet do not call for the rejection of any of the empirical discoveries or conceptual advances made in molecular biology since the 1950s. Similarly, we argue individual tenets of the Modern Synthesis can be modified, or even rejected, without generating a fundamental crisis in the structure of evolutionary theory – just as the Modern Synthesis itself improved upon but did not cause the rejection of either Darwinism or neo-Darwinism. (Pigliucci & Müller, 2010a: 9-10)

This is an odd rendition of the Central Dogma, that specifically neglects a major 1970 paper by Crick in which he discusses his original 1958 version of the idea and then modifies it (Crick, 1970). In its original formulation and its modified version, viral RNA replication, DNA \rightarrow protein, RNA \rightarrow DNA, and the role of prions were all discussed and incorporated. What were ruled as unlikely were data flows from protein to RNA or DNA. In Chapter 7 I discuss the Central Dogma and the detail of this 1970 paper in the context of epigenetic processes, an area that a number of advocates of the Extended Synthesis have explored.

In spite of this quibble, I agree with the broader point that we can see the transitions from Darwin to the Modern Synthesis as modifications, and that those modifications left intact much of the original work, but not all. And it is certainly the case that these transitions did not lead to crisis, but they did lead to robust disagreement and the formation of distinct interest groups, for example the biometricians and Mendelians of the early 20th century, whose debate proved useful (Chapter 3). We might package this as *dissent with modification* and note that this is normal business for any science. And put this way we get a sense of what Pigliucci and Müller meant about consistency – for them, modification is a process that gradually shifts you from the original form toward something new, an evolutionary process in its own right. At some point the emerging novelty is consistent with early ideas, whilst different enough to warrant a title: *what is it we should call this conceptual space?* And as you might expect, Pigliucci and Müller provide a diagram to denote this spatial relationship (Love, 2017), and have the Extended Synthesis encapsulating the Modern Synthesis, which in turn encapsulates Darwinian evolution (Pigliucci & Müller, 2010a: 11) (Fig.1.1).

INSERT FIGURE 1.1 ABOUT HERE

If I am right, then the claim of Pigliucci and Müller is a claim to novelty and they characterize novelty predominantly in terms of phenomena previously unaccounted for by the Modern Synthesis but also in terms of a move away from traditional views of the role of natural selection and the nature of adaptation, inheritance and replication, developmental biology and the informational role of the gene. These shifts, they argue, are a result of novel discovery and inclusion.

Pigliucci and Müller are engaging in a taxonomic exercise. They are listing features, and processes, that differ between the Modern Synthesis and the conceptual space that has since emerged. They feel ready to declare a new species of theory, the Extended Synthesis, which is historically contingent and thus conceptually related to, or consistent with the Modern Synthesis, but the two are moving toward

reproductive isolation. And yet, using the same data about new ideas in evolutionary biology, emerging from new phenomena, it would be possible for our conceptual ecologist to track a gradient between, for example, those adopting adaptationist programs of research in behavioral ecology which emerged in the final stages of the Modern Synthesis (Chapter 3) and those interested in phenotypic plasticity expressed under various conditions.

In this book I discuss multi-level selection (Chapter 3), phenotypic plasticity (Chapter 5), evolutionary developmental biology (Chapter 6), epigenetics (Chapter 7) and niche construction theory (Chapter 8) as these areas have provided core phenomenological claims for advocates of the Extended Synthesis, and feature heavily in the major book length treatments of this advocacy (Huneman & Walsh, 2017; Pigliucci & Müller, 2010b; Uller & Laland, 2019a). What is notable about these areas is how they can be lined up on a gradient organized from a focus upon *population* thinking to thinking about *form*.

Darwin is attributed with the introduction of population thinking, making evolution a kind of change that happened to populations and not to individuals. In doing this he stepped away from a transformationist notion of development and evolution as closely related, if not identical processes. Lamarck's commitment to the inheritance of acquired characters was to a developmental process at the individual level, mediated by behavior to a large extent, that fitted the form of an organism to the environment in order to solve crucial problems. This was his notion of adaptation, and he was metaphysically committed to such changes being heritable. Evolution was the change in form within species over time as a result of such processes. For Darwin, the population changed due to the differential success of variants in the struggle for life. Variants were of form, and his struggle was to understand the sources of variation, as well as the mechanisms of inheritance, but this clearly posed a different problem to that considered by Lamarck. Darwinian evolution was not about changes in form, but rather how changes in form could lead to changes in populations. Ultimately, those populations could be characterized by the predominant forms present and those forms, duly selected, were adaptations.

The arrival of neo-Darwinism and then the Modern Synthesis gave a mechanism of inheritance that enhanced Darwin's view. And in so doing it allowed a new direction of gaze, from the gene up. The gene was clearly a crucial element for development *and* for the evolutionary process, and thus had a role to play in the emergence of form ontogenetically and its ordering phylogenetically. This direction would feel familiar to Lamarckian thinkers, but the difference was that Darwinians had their eye always upon population change.

In Figure 1.2, I have depicted one possible hypothesis about how the central themes used by advocates of an Extended Synthesis might relate to one another along a continuum from *population* level accounts to accounts focused upon the emergence of *form*². I take the population end of the continuum to be traditionally

² A related idea about a transition from theories of form to theories of genes has been mooted in the literature (Pigliucci, 2007), and I shall return to this idea in §1.1.3.

Darwinian, and also the focus of the Modern Synthesis. As a result I have positioned Multilevel Selection Theory close to that pole. Niche Construction Theory, with its focus on the effect of organism activity upon population level selection dynamics, is also toward that end of the continuum. But these theorists also discuss the role of agents in the creation of their own form. Evolutionary Developmental Biology sits in the middle with a clear interest in the role of the development of form upon selection dynamics at the population level. Epigenetics is closely related to this discipline, but its principal role is in gene regulation and thus the expression of form. Nonetheless, epigenetic transmission has been recruited to selection-based arguments by some. Finally, plasticity is all about the reactive nature of form with relation to the environment, and whilst a part of the developmental response it is often recruited across arguments for the Extended Synthesis, in part as a counter to gene-centrism and notions of formal determination. This is why it occupies a place near the *form* pole.

INSERT FIGURE 1.2 ABOUT HERE

What Fig.1.2 does not yield is an account of the direction of travel for those engaged within each of the core areas. It is presented as a possible gradient based on the observations of this conceptual ecologist. Using this continuum, it is possible to come to a phenomenon such as plasticity and ask whether this capacity has been selected. Answering this question would not preclude further exploration of the impact of plastic responses upon selection dynamics. Indeed, that would inevitably become a part of that account. Similar questions could be addressed within epigenetics. Some may be surprised to see me separate Evolutionary Developmental Biology from plasticity and epigenetics, after all these are mechanisms involved in development. This is true, but there is more to development than this and a key argument from Evolutionary Developmental Biology has been around the conserved, compartmentalized nature of development and what this might mean for evolution. This is why I have positioned this field slightly left of center in the figure. Nonetheless, it is still possible to arrive at the facts of compartmentalized development and ask whether this trait has been selected.

From left to right is the direction of travel for those applying the Modern Synthesis (Fig.1.2). My suspicion is that many seeking an extension of the synthesis start their journey somewhere toward the *form* end of the continuum and head toward the other pole, in much the way Darwin had to when confronted by the diversity of life. Where Darwin invented this for himself, modern scholars are armed with Darwinian theory, and know to look for mechanisms of inheritance and the production of variation. As they travel leftwards, they reveal various localized levels of mechanism that produce form and sit well above the level of the gene. Naturally they wonder whether or not these levels are both necessary and sufficient for the production of *form*, and because there is variation at these levels they wonder if some kind of general Darwinian process might unfold (§1.1.2 (Webb, 2011)). For this they would need inheritance, and within the epigenetic and niche construction

literatures there is much discussion of non-genetic inheritance and how that might enable evolution.

This use of Fig.1.2 is highly rhetorical. I cannot hope to truly fathom the real starting points and motivations of each and every one of those advancing arguments for an extension of the Modern Synthesis. But my hope is that it makes for a useful tool, to at least pry open the discussion and delve into the mechanics of the arguments. For example, thinking about travel from *form* toward *population* accounts, I can see how readily a scholar might stop and read gene-level theorists and wonder how on earth they truly believe that the data contained within a gene can account for the diversity and complexity they see from their perspective. Gene-level theorists might easily appear to be utterly detached and esoteric in their accounts. But just as they accuse others of privileging the gene, and gene-centrism, they effectively privilege developmental processes, sidelining a core element of continuity. This is something often excused by claiming that the Modern Synthesis deliberately left development out of the unification of biology and arguing that it is now time to prioritize these processes and to see if they do more than explain ontogeny (Chapters 4 and 6).

Fig.1.2 is no more rhetorical than Fig.1.1. Pigliucci and Müller's (2010a) placing of multilevel selection theory and niche construction within the extended synthetic set conveniently ignores the fact that group selection ideas occurred within the period of the Modern Synthesis (Wynn-Edwards, 1962) and that Darwin discussed the core concepts of niche construction in his work. Moreover, plasticity has received considerable theoretical attention from scholars within the Modern Synthesis. I suspect some of these oversights are also a consequence of travelling from the *form* end of the continuum and arriving at these ideas before fully immersing oneself in the role of the gene and *population* thinking. But the inclusion of multilevel selection is puzzling as this relies upon Darwinian selection, fitness and population level change. This is clearly a Darwinian view at base, and proponents such as Wilson recruit single gene models in keeping with the phenotypic gambit from behavioral ecology, a product of the Modern Synthesis (Grafen, 1984; Wilson, 1975). All told, this does not appear to be a radical departure from standard theoretical thinking.

One reason that some may choose to start with *form* is that they wish to counter claims that natural selection is the preeminent creative force in evolution. Developmental processes can be invoked by those proposing an extension, in order to discuss the potential limits on available variation in a population (Lewens, 2019). Lewens sees this as a mild claim, that does not particularly challenge the Modern Synthetic view that natural selection underlies the emergence of adaptation. Indeed, a clear relationship between an underlying selection dynamic and available variation constrained by developmental factors would make for what Lewens' terms an *enriched* account of a given phenomenon. But Lewens also points to a stronger reading of the view that development is involved in the creation of adapted form. This rests on processes like learning that enable an adaptive fit during ontogeny. Lewens is quick to point out that whilst the precise outcome of a learning event might not be something selected in ancestral conditions, the capacity to learn may

well be so, and in so doing he is in keeping with standard theoretic views of plasticity (Chapter 5).

In making this last point, Lewens gives an imaginary example of an animal learning to avoid a novel predator. This learning is labelled adaptive, providing an adaptive fit, and my reading of his paper is that this is supposed to capture the idea of adaptation, thus *adaptive* is used as a synonym for *adapted*. I think this use of adaptive, which is common on both sides of the debate for simple reasons of common usage, is potentially perilous. Adaptive means given to, or prone to adaptation, which in turn is about adapting, or modifying to new purpose or adjusting to new conditions (Stevenson, 2010). This notion of modification and adjusting is another view of plasticity. Within evolutionary biology we can talk of populations adapting, and more generally of populations being prone to adaptation, where adaptation is a technical term. Populations are then adaptive or plastic, and under Darwin and the Modern Synthesis, are the proper focus of attention. But, whilst it is true that, for example, behavior enables organisms to adjust and modify in light of new conditions, this does not carry with it any technical evolutionary connotations – or rather, it should not until extra conceptual work has been done. In evolutionary terms, where we regard a species trait as an adaptation, we regard it as a trait with a positive fitness function. Not all behavioral responses will contribute to average lifetime inclusive fitness and Williams advised us, in his contribution to the Modern Synthesis, to take the work of identifying adaptations seriously and cautiously (Williams, 1996).

To return to Lewens' example, the animal learns to avoid a novel predator most likely because core indices of predation threat are present in that animal. Being able to use those indices as data in an appropriate learning response is a credible adaptation that allows adjustments in the present by the potential prey item. In strict evolutionary terms, in keeping with the Modern Synthesis, the adaptation is the learning mechanism and the particular *token* behavior that releases the animal from threat is not. However, we might be able to say that that *kind* or *type* of behavior is an adaptation, but in so doing we are in fact describing some of the parameters of the mechanism that delivers it. Most typically, in this latter case, we would describe it as predator evasion behavior. For learning to work, as what Lewens terms an exploratory process, error will also be produced by these mechanisms and we have no reason to label errors as evolved adaptations, especially as they may be costly.

I think being clear about these distinctions is important because noting adjustment and modification is not the entirety of noting adaptation in the strict evolutionary sense. Ironically, the looser uses of adaptive enforce a kind of pan-adaptationism upon explanations in the absence of evidence, something which the forebears of the current arguments for extension worried about (Gould & Lewontin, 1979; Gould & Vbra, 1982). I strongly suspect that where some see adaptive fit between an organism and the world, they by default assume adaptation and thus evolution. Moves by learning theorists, to model learning as a form of selection by consequences, may have enhanced this view (Smith, 2018). This perspective is

again a consequence of travelling from *form* toward *population* on the continuum in Fig.1.2, whilst having in mind knowledge of what Darwinian evolution is.

1.1.2 Further abstractions

Webb (Webb, 2011) has proposed a distinction between a General Theory of Evolution, that applies to “order-generating evolutionary mechanisms you might find anywhere” (p.94) and the Special Theory of Evolution, which is a “particular worked example of the General Theory” (p.94) that he aligns with the Modern Synthesis.

Webb’s general theory covers systems that meet six criteria.

1. *Information*. An information base, where information content is associated with differential instantiation.
2. *Variation*. Variance within that information, not just as a starting condition but recurring, by whatever mechanism (such as copying errors) or by introduction from elsewhere.
3. *Recombination*. Some de facto recombination of the information taking place, in which the “shuffling” of informational components is associated in some systematic way with the differential instantiation.
4. *Selection*. Selection against some vaguely persistent criteria, that leads to differential distribution of the information according to its differential instantiation.
5. *Replication*. Some form of copying, or relative increase, or privileging, whereby the information redistributed by selection differentially and systematically changes its frequency in the system.
6. *Iteration*. Multiple repeats of this sequence. As a consequence of this the altered frequencies resulting from replication and selection bias the pool in which variance and recombination are occurring. (Webb, 2011: 96)

He notes that biological systems enable these criteria, but so can non-biological systems. He gives as an example the high throughput method used in the pharmaceutical industry where chemicals are thrown at bacterial cultures to see if there is a desired effect. The only thing known prior to this process are the formulae of all the chemicals that will be tested. Once an effect is discovered the scientists look up the formula of the responsible chemical, synthesize lots of variants on this theme, do lots of “mixing and matching” (p.99), transmitting what works to the next generation of tests, and gradually winnow options toward a candidate drug for their target problem.

It is possible that this distinction might make immediate sense of Fig. 1.1, and Pigliucci and Müller’s (2010a) notion of consistency between Darwinian theory, the Modern Synthesis and their proposed Extended Synthesis (Dickins & Dickins, 2018). Whilst Darwin was focused upon naturally occurring biological systems, he drew heavily upon lessons from animal breeders and also Malthusian ideas about population dynamics. The use of these examples might be seen as reasoning by analogy (Evans, 1984; Gildenhuis, 2004; Theunissen, 2012), and the analogy worked because there is something in this general process that can bring order to

systems. It was perhaps less analogy, and more homology. The development of the Modern Synthesis, or the Special Theory of Evolution, was then a detailed effort to understand precisely how naturally occurring biological systems, known as populations, were organized according to these generic principles. Thus, the Modern Synthesis is a consistent extension of Darwinian theory within the biological realm. But what of the proposed extension to that synthesis?

Moving from left to right along the continuum depicted in Fig.1.2, from *population* concerns to those of *form*, would enable a ready accommodation of all of the phenomena and areas listed. There are available accounts of all of these things that are entirely consistent with the Modern Synthesis, and I attempt to demonstrate this throughout the relevant sections of this book. But for those travelling in the other direction, as noted above, there is a temptation to look to non-genetic sources of variation and inheritance and to argue for evolutionary dynamics as a result. These evolutionary dynamics might be claimed to continue independently of gene-level selection, such as in models of learning that rely on selection by consequences, or cultural evolution models that rely upon social learning mechanisms. Indeed, Dawkins, the arch villain of gene-centrism famously made this point about cultural evolution when he mooted the idea of memes as a form of conceptual replicator (Dawkins, 1989). Here we might lay claim to the General Theory of Evolution as a possible account of the emergence of order in the relevant cultural systems, but Webb would expect these accounts to conform to his criteria.

We can follow the preceding suggestion a little further. Either scholars declare non-genetic evolutionary processes to be general evolutionary processes that make no contact with the underlying processes that are the business of the Special Theory of Evolution, or they must claim some kind of relationship between General and Special processes. If the claim is for a relationship that can take the following forms: (i) feedback into selection dynamics or, (ii) the narrowing of exploration space.

General processes could establish order that in turn establishes selection dynamics, which amounts to a feedback at the population level. An example of such a claim might rely upon social learning mechanisms delivering particular behavioral outputs in a stable environmental scenario, and those outputs constraining aspects of the environment. The lactose tolerance story, so often used by niche construction theorists, is a case in point (Scott-Phillips et al., 2013). Accordingly, humans learnt to use milk products as energy and nutrient rich food sources, and in so doing increased selection pressures for alleles that did not switch off lactose tolerance in infancy. As a result, adult lactose tolerance increased within certain subpopulations. This form of niche construction has been labelled selective (Uller & Helanterä, 2019).

General processes can produce stable phenotypes simply as a consequence of prior *special* processes leading to the selection of adaptations. Those adaptations narrow phenotypic range at physiological levels (including behavior). Lewens' point about the selection of learning mechanisms to allow learning can fit this category (Lewens, 2019). If, for example, learning is a process of selection by

consequences than that learning is a result of those evolved mechanisms, but the selection dynamics that unfold at the learning level are independent of prior selection for the mechanism. This is, in fact only partially true as we should expect constraints on the type of learning and thus the type of thing that can be learnt. Nonetheless, behavioral variation can be instantiated. Whilst learning in this context is an individual level process, we should note that the General Theory approach does not stipulate that systems must be populations.

I am not claiming these two kinds of relationship to be exhaustive. Rather I am pointing out that there is a separation and also possible interaction between general evolutionary and special evolutionary systems. But interaction depends upon the systems working as they do. There is no sense in which the operations and outcomes of cultural learning change how selection can favor particular alleles.

1.1.3 Explanation

If advocacy for extension were merely advocacy for recognition of specific interactions that have been noted during investigations into the ontogeny of form, then it would be no more than a claim for additional and interesting topics of study. This is not normally something that requires the endorsement of theoreticians in an enormous and critical literature. Nonetheless, I suspect this is precisely how many biologists read it, and it explains the common “so what?” response that Pigliucci and Müller reference (§1.1.1 (Pigliucci & Müller, 2010a)). As we have seen these particular authors reduce this to an issue of consistency and argue that consistency does not mean identity, which is of course true. In §1.1.1 I gave some possible interpretations of what is meant by consistency. They were the addition of missing, or deliberately evaded, fields of study and the focus upon the emergence, or creation of *form* as an analytic starting point. These interpretations, either independently or together, give the impression that advocates of extension see the Modern Synthesis as a categorical statement of interests, and anything additional will have to be an extension. It then becomes a moot point of epistemic arithmetic as to when continued addition leads to a qualitative shift in scientific enterprise.

Some advocates directly address the idea of qualitative shifts, in the context of paradigm shifts, following Kuhn, and modifications to the outer belt of auxiliary hypotheses, following Lakatos and in so doing raise another aspect of calls for extension: does a different phenomenal focus force change upon the structure of evolutionary explanations (Baedke, 2021; Dickins, 2020; Otsuka, 2019)?

The most recent book length treatment from those seeking extension focused upon the issue of causation in evolutionary biology (Uller & Laland, 2019a). This book covered a diverse array of topics, including issues to do with development, plasticity, and niche construction. In my review of the book, I made the following claim, in response to a point from Uller and Laland about the nature of models as abstractions that result from choice of focus (Uller & Laland, 2019b):

The MS is indeed a framework to deliver models. Its core conceit is the definition of evolution given by Darwin, and it has relied upon natural selection to generate hypotheses. But the MS has not been unaware of other ways to produce patterned population change, and drift is always to be considered for example. What natural selection does is enable the construction of falsifiable hypotheses about particular biological systems. As such, the MS might be seen as a viable research program, following Lakatos. As a viable research program, new discoveries about the origin of variation, or competition or inheritance are to be dealt with—do they challenge the hard-core axioms of the program, or can they be accommodated, even with tweaks to the protective belt of day-to-day empirical work? To challenge new predictions must be made. (Dickins, 2020: 513)

In this case, Uller and Laland were hoping to emphasize the point that other creative forces are involved in the production of form. I went on to suggest that perhaps the claims for extension could be seen as viable modifications to the protective belt, but not as challenges to the core axioms of the Modern Synthesis. In this way, I made sense of the claims for additional phenomena but drew upon Lakatos to make the point that a qualitative shift had not been achieved.

Baedke (2021) has pulled me up on these comments. In his paper he wonders “why, at all, should a critique of evolutionary biology only be considered a valid contender or ‘real challenge’ if it criticizes (or tries to falsify) the theory of natural selection?” (p.85). Baedke claims that an axiomatic approach to understanding theory change sets the bar too high for critics. I find this response perplexing as I am not entirely sure why anyone should make life easy for critics. Moreover, I was simply responding to arguments from within the volume that directly referenced Lakatos, and other discussions of research programs. Thus, Otsuka claimed that the Modern Synthesis is showing signs of degeneration, in keeping with a Lakatosian perspective, and has issued “ad-hoc patches just to save its core doctrines without leading to novel research questions or predictions” (Otsuka, 2019: 262). Otsuka’s analysis is that the Modern Synthesis is being outcompeted by the rival Extended Evolutionary Synthesis research program. My view of the scene suggested a different use of Lakatos, not least because as Baedke points out I see developmental explanations as separate from evolutionary ones such that evolutionary axioms are in some senses impervious to developmental accounts (Chapter 4 and 6).

Toward the end of the paper Baedke advocates for pluralism, for the incorporation of developmental accounts into evolutionary theory, and a focus upon desirable features of explanatory power. In doing this I suspect his journey is from *form* toward *population* (Fig.1.2) because he does not seem to consider the alternative that development is something to be explained by evolutionary theory, rather than made part of it.

In another paper Baedke and colleagues analyze the nature of explanation at stake in this debate (Baedke et al., 2020). Here they directly discuss Pigliucci’s comments about theories of form and genes.

I will provide a brief conceptual recapitulation of the history of evolutionary theory, with the aim of tracing the broad questions posed by evolutionary biologists at different points in time during the past 150 years, as well as the sort of approaches that have been used to

answer such questions. I will then argue that evolutionary theory has shifted from a theory of form to a theory of genes, and that it is now in need again of a comprehensive and updated theory of form. (Pigliucci, 2007: 2743)

As Baedke et al. note this is something that has also been described as a shift from statistical correlation to mechanistic causation (Pigliucci & Müller, 2010a) and as something that opposes population thinking. This suggests that Fig.1.2 at least describes some aspect of the debate, and I am probably right about Baedke's direction of travel. Their view is that differing ideas of what constitutes explanatory power are in fact in play such that advocates of extension, like Pigliucci, are arguing for both complementarity between the Modern Synthesis and an Extended Synthesis, but also for increased explanatory power with the addition of this complement.

Baedke et al. claim that explanatory power "can be assessed by comparing the range of inferences to potentially new counterfactual situations and, accordingly, of answers to w-questions that alternative explanations make possible" (p.7). W-questions are *what if things had been different* questions. As an example, they suggest that an account of a population dynamic might have been made more counterfactually comprehensive with the introduction of developmental factors. They dub such expanded explanations more informative. This relates to the idea of *precision*, which is an outcome of the amount of detail, perhaps from across levels of biological organization, that is incorporated. Baedke et al. note that this is decreased by *idealization*, such as that found in modelling practices (Potochnik, 2020) and they further claim this can lead to false answers to counterfactual questions.

"Another criterion for saying that explanations are better argues that they should cite causes *proportional* to their effects, meaning that they have the same degree of precision and thus level of analysis" (Baedke et al., 2020: 9, italics added). An example here might be the developmental claim that relying on genes alone to explain form is not proportional to the effects seen in the emergence of form. Again, this is an aspect of detail. The addition of detail not only facilitates *precision* and *proportionality*, but also *sensitivity* such that more detailed explanations are more sensitive to changes in background conditions and context, and thus less readily generalized.

Baedke et al. recruit these principles to look at explanations from the Modern Synthesis and alternative accounts proposed as a part of an extension. What they immediately note is that both differ with respect to *precision* about what it is to be explained. This is because standard theory "focuses on genes and populations and abstracts away from details on the organismic level" (p.12). By this they mean that an extended synthesis can "provide information about cultural niche construction, social learning, sources of variability, directionality, causality, modes of inheritance, targets of selection, and tempo of evolution" (p.13). When discussing *idealization*, they use optimal foraging models as highly idealized standard theory models and contrast this with an extended approach that does not assume individuals are rational maximizers. They draw a moot point about distinctions in proportionality between standard and extended approaches.

The entire analysis from Baedke and colleagues is designed to show which explanation is better, a standard, Modern Synthetic one or one from an Extended

Synthesis. But they make clear that both camps are in fact trying to explain something different, which makes comparison with regard to efficacy redundant. A question about whether or not a trait is an adaptation is not the same as a question about how that trait develops ontogenetically, nor about the phylogenetic history of its emergence.

Ontogeny and phylogeny can provide useful clues to determining the adapted value of the trait. The use of those clues, and also the error in behavioral signal that can be measured by using optimality models, is all part of the practice of biologists that emerged from the Modern Synthesis. Thus, optimality models are used to idealize the functionality of hypothesized foraging behaviors and to define parameters in terms of inclusive fitness theory. Those models are applied to real animal behavior. The expectation is that actual behavior will be suboptimal and the next step, for behavioral ecologists, is to develop hypotheses about the causes of that suboptimality. But Baedke et al. complain that this practice uses plasticity incorrectly, by seeing it as a further mechanism for fitness maximization. It is true that fitness maximization is a core axiom of inclusive fitness theory, which emerged from the Modern Synthesis (Chapter 3). The addition of plasticity to an optimality model, under this axiom, is the addition of detail to the model, which allows for some sophisticated, and *precise* claims about the functional parameters of mechanism (Nettle & Bateson, 2015). However, it is also the case that behavioral ecologists expect some error to be chaotic and possibly unavoidable under certain circumstances. Here Baedke et al. would further complain that this approach is externalist and allows no interaction between what is within and what is without in an account of form (Godfrey-Smith, 1996). The environment drives it all.

Baedke et al. are probably right that the addition of detail to an explanation can make its prediction more precise, and as a result of that the probability of very precise outcomes are reduced, making those outcomes more surprising and therefore more informative when they do happen (Chapter 5). But those details have to be the right details for the task at hand. Simply noting that an Extended Synthesis would add more details is not sufficient to endorse this as an explanatory strategy. Evolutionary theory is not about the emergence of form, but the selection of form. How form emerges is of no relevance, but that it does is. But, of course, how form interacts with the world impacts upon selection. Whilst it is the case that phenotypic variation is caused by both genetic and other causes during ontogeny, it is the likelihood of those ontogenetic effects being wrought consistently across time that allows evolution. The Modern Synthesis taught us that genes have this property of consistency, whereas ontogenetic exposures do not for reasons to do with the vicissitudes of life but also to do with the nature of individuality. This suggests that genes must be able to cope with a deal of noise in their systemic interactions with the world, but as natural selection shows this has its limits (Dickins & Dickins, 2008). A clear counterfactual that Baedke and colleagues more generally ought to deal with is whether or not evolution could occur without a necessary antecedent cause like the gene? Also, could evolution occur without niche construction, plasticity and so forth? If the answer to this first question is “no,” and to the last “yes,”

then it becomes clear that niche construction, plasticity and so forth are not a necessary or sufficient part of evolutionary theory.

1.1.4 Information

This brings us to the central theme of this book, and that is information. In Chapter 5 I introduce information and draw a distinction between data and information such that *information = data + context* (cf. (Floridi, 2010)). This allows me to draw a further distinction between notions of *information as something in the world to be harvested* and *information as a functional relationship between data and context*. It is this last view that I endorse and that I recruit to make sense of the Modern Synthesis and particular interpretations of it by those seeking an extension. Very simply put, organisms do not seek information, but they produce information by processing data that they are designed to respond to. But this is a view that does not just account for organisms but also for their component parts and can be applied within evolutionary and developmental contexts. A part of my claim is that life is information, or rather creates it, and that the patterned use of inputs from the world external to a given system demands an explanation in these informational terms. It was this that the Modern Synthesis provided, and it is this question that developmentally oriented advocates of an extension cannot avoid but have in fact tended to. But, as I explain in the book, a large part of this ignorance is due to the colloquial use of *information* as out there, to be harvested, and both sides of the debate adopt this usage.

To treat the gene as conveying developmental information is to use information in error. Genes contain data, and that data only has an informational role within the context of a developmental system (Oyama, 2000). This idea is present within core writings of the Modern Synthesis, but the distinction between data and information is not drawn and, I claim, has led many to misunderstand the role of the gene in standard theory. The gene-centrism of that theory is not a commitment to total developmental determination, to some kind of preformation, but rather to a necessary data input at the start of a complex, multi-systemic response that does deliver form. The concept of the gene that is really at work in the Modern Synthesis, is one that enables this necessary input and delivers the constancy across time that it is essential for evolution as a population level effect. So, the optimality models of foraging theory rely upon this notion of constancy and data in the abstract to enable their hypotheses about behavior, but there is no commitment to the totality of the behavioral response being encoded within a gene, but rather to a complex set of genes catalytically contributing to a long developmental process. Genetic data is at the bottom of a hierarchy of multiple constraints upon the kinds of behavior an organism can produce, not the precise tokens.

The astute reader will note that this use of information is framed as travel in the direction of *form*, from left to right in Fig. 1.2. As such it is a commitment to statistical correlation, but it is also a commitment to a particular functional account of

the mechanistic causes of diversity and form. It provides the explanatory parameters for developmental accounts and in this way the Modern Synthesis has always incorporated the phenomena that those advocating extension claim are forgotten. Some describe this as a process of black-boxing the true mechanics of development etc. but as I argue in this book that black-boxing, or bracketing proved prescient and the phenomena of development that are presented for the extension are entirely in keeping with the fundamental axioms of the Modern Synthesis; the black boxes were the right size and shape.

1.2 Summary

This book represents my interpretation of evolutionary theory and modern debates about its adequacy. I have used multiple sources and doubtless drawn conclusions and inferences that many, including those who consider themselves aligned with the Modern Synthesis, would find puzzling and in error. Those errors are honestly achieved. For the most part variance in my error will be intrinsically caused, as for everyone. Those intrinsic causes will include intellectual shortcomings but also my learning history over long exposure.

My professional discipline is behavioral science, and I am especially interested in what behavior is and is for. This has naturally drawn me to evolutionary accounts, and most especially those from behavioral ecology. But I also have a background in history and philosophy of science, and I have long held an interest in just how theories work and are applied. This is another reason for my attraction to evolutionary theory. Finally, I also have some training in ecological methods that I mostly put to use in bird surveys. It was reflecting upon this list of interests and trying to find a common thread that led me to realize I was a *conceptual ecologist* when addressing theory. Whilst trained in history and philosophy of science I would argue that my approach to the project of this book, and the prior papers that led to it, was one of surveying, classifying and organizing. My interest in information theory has many routes, but one is its use in diversity indices in ecological surveys. Here I try to weave information theory into my arguments, and adopt it as an organizing principle, although I think it has theoretical potency also.

The book begins by retelling the history of evolutionary theory from Darwin to the end of the Modern Synthesis (Chapters 2 and 3), which I place around the mid 1970s, when Dawkins gave us the replicator-vehicle concept. This history draws upon the same narrative arc that many, on both sides of the debate about the Modern Synthesis commit to but I also include discussion of multilevel selection theory and inclusive fitness. I am aware that there are other histories to be told, that have been told, and I think this is another way into the debates at the core of this book but one I am not skilled enough to produce.

After the history I then deal with some core explanatory issues. First comes causation (Chapter 4) and in particular I focus upon Mayr's detailed working of the

proximate-ultimate distinction and recent critics of this. I regard Mayr's classic paper on this topic as a central philosophical statement of the Modern Synthesis and given the amount of critical effort directed toward it my impression is that I am not alone. In Chapter 5 I introduce information in the context of plasticity, although this topic receives treatment throughout the remainder of the book.

Chapters 6, 7 and 8 then deal with arguments from those advocating for an Extended Evolutionary Synthesis. They are evolution and development, epigenetics and niche construction theory. In each chapter I focus on some core positions in these fields, well aware that I cannot do justice to the volumes of fascinating material accumulated under each topic. But my hope is to pull out the kind of reasoning at work, and to contrast that with my own interpretation drawn from my views on information among other things. In chapter 9 I bring all of this together with further discussion of information and also developmental systems theory, leading to a statement of my current position with regard to the issues at hand.

I have necessarily missed various arguments from my book, taking what might be seen as the developmental route through the extended synthetic claims. I do not discuss evolving genomes, macroevolution, the major transitions nor issues emerging from structuralism. This does not indicate a lack of interest, but rather a decision about how to make my case. I may return to these issues at a later date.

1.3 Conclusion

This book argues against an extended synthesis, but it does not represent the only way to do this. In making a negative case I am not attempting to disparage the enormous efforts made by those advocating for extension. To leave a theory uninspected is irresponsible. They are products of their time and new discoveries may well challenge them, and at some point, make clear that change is required. Those working for extension are doing this and causing those of us who disagree to think long and hard about why we do. The Modern Synthesis is a framework theory, as I discuss in the final chapter, and is a product of work over an extended historical period. That makes its inspection and analysis difficult but rewarding work. My hope is that I engage the reader just as I have been engaged by all whom I cite.

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