



Mayr and Tinbergen: disentangling and integrating

Brandon A. Conley¹

Received: 22 August 2018 / Accepted: 6 December 2019
© Springer Nature B.V. 2019

Abstract

Research on animal behavior is typically organized according to a combination of two influential frameworks: Ernst Mayr's distinction between proximate and ultimate causes, and Niko Tinbergen's "four questions" (mechanisms, development, survival value, and evolution). My aim is to debunk two common interpretive misconceptions about Mayr's proximate–ultimate distinction and its relationship to Tinbergen's four questions, and to offer a new interpretation that avoids both. The first misconception is that the proximate–ultimate distinction maps cleanly onto Tinbergen's four questions, marking a boundary between Tinbergen's evolutionary and survival value questions (ultimate) versus developmental and mechanistic questions (proximate). The second is that Mayr's proximate–ultimate distinction is meant to rule out the relevance of proximate causes to evolutionary explanations. I argue that neither is plausible given the text and Mayr's philosophical aims, namely, to argue that evolutionary biology cannot be reduced to either the physical sciences or to other areas of biology. Through a reconstruction of Mayr's anti-reductionist argument, I develop an interpretation according to which the proximate–ultimate distinction marks two ways that teleological reasoning can be naturalistically grounded in biology, corresponding to Mayr's distinction between teleonomic and adapted systems. Mayr distinguishes reduction, which the proximate–ultimate distinction is meant to block, from analysis, through which he allows that proximate causes, causes that are neither proximate nor ultimate, and chance can all contribute to evolutionary explanations. I conclude by suggesting some ways in which the interpretation defended here reframes our understanding of Mayr's disagreements with some evolutionary-developmental biologists.

Keywords Ernst Mayr · Niko Tinbergen · Proximate · Ultimate · Four questions

✉ Brandon A. Conley
bac248@cornell.edu

¹ Department of Philosophy, Colgate University, Hamilton, USA

Introduction

Research on animal behavior is typically organized by a combination of two influential frameworks: Ernst Mayr's distinction between proximate and ultimate causes (Mayr 1961, 1974, 1982, 1984, 1988, 1992b, 1993, 1996, 1997, 2004), and Niko Tinbergen's "four questions," concerning mechanisms, development, survival value, and evolution (Tinbergen 1963). My aim is to debunk two common misconceptions about Mayr's proximate–ultimate distinction and its relationship to Tinbergen's four questions.

The first is that Mayr's proximate–ultimate distinction marks one of two axes dividing Tinbergen's four questions (Sherman 1988; Holekamp and Sherman 1989; Alcock 1993; MacDougall-Shackleton 2011; Bateson and Laland 2013; Nesse 2013; Taborsky 2014; Hofmann et al. 2014). Survival value and evolution are grouped together as ultimate while development and mechanisms are grouped as proximate. The other axis divides the non-historical, mechanisms and survival value, versus the historical, development and evolution. This picture of the relationship between Mayr's and Tinbergen's frameworks is ubiquitous, though not universally accepted (Dewsbury 1999 rejects it), and it plays an important pedagogical role (see especially Alcock 1993; Nesse 2013). I thus refer to this picture as the "Standard View." It is summarized in Fig 1.

The second misconception is that, by definition, only ultimate causes are relevant to evolution, so the proximate–ultimate distinction precludes the possibility of integrating Tinbergen's four questions. Mayr's proximate–ultimate distinction features prominently in debates about the cogency and import of various integrative

Fig. 1 The Standard View of the relationship between Mayr's and Tinbergen's frameworks. Parenthetical terms are common alternate labels

	Non-Historical	Historical
Proximate	Mechanisms (Causation)	Development (Ontogeny)
Ultimate	Survival Value (Function)	Evolution (Phylogeny)

research projects, most notably evolutionary psychology and evolutionary-developmental biology (evo-devo). Though my goal is to defend a historical interpretation of Mayr's views, this work is in part motivated by its relevance for clarifying these debates.

After summarizing the two frameworks, I offer several criticisms of the Standard View. It cannot capture the role of history in Mayr's characterization of the proximate–ultimate distinction. It also lacks textual support and fits uneasily with other historical evidence. Finally, the Standard View renders the proximate–ultimate distinction ill-suited to do the philosophical work Mayr invokes the distinction to do. I then summarize the apparent tension between Mayr's use of the proximate–ultimate distinction to defend the autonomy of evolutionary biology, on one hand, and Tinbergen's challenge to integrate his four questions on the other. I argue that contrary to several commentaries (e.g. Amundson 2005; Laland et al. 2011; Calcott 2013a, b; Laland et al. 2013a, b; Scholl and Pigliucci 2015), Mayr did not take development to be irrelevant to evolution.

The rest of the paper is devoted to developing a positive interpretation of the proximate–ultimate distinction, the role it plays in Mayr's larger view, and how it can avoid the two misconceptions. According to the interpretation I defend, proximate and ultimate causes represent two ways of grounding teleology, or end-directedness, in biology. Proximate causes are the inputs and operations of a computational program realized in the organism while ultimate causes are contributions to fitness favored by a history of natural selection. Proximate causes, causes that are neither proximate nor ultimate, and chance can all contribute to evolutionary explanation through a process of analysis, which Mayr is careful to distinguish from the reductionism he seeks to undermine. I argue that Mayr and Tinbergen share a conception of integration via a process of analysis akin to Robert Cummins' (1975). I conclude by briefly discussing how the interpretation developed here informs our understanding of Mayr's debate with some evolutionary developmental biologists.

Overview of the two frameworks

Mayr introduced the proximate–ultimate distinction as part of a philosophical defense of the autonomy of evolutionary biology from molecular biology (Beatty 1994; Mayr 1994). By 1961, when Mayr published “Cause and Effect in Biology,” in which the distinction is popularized, molecular biology was rapidly monopolizing funding, academic positions, prestige, graduate students, and publications. In response to a growing sense that all biology would be reduced to molecular biology, and in turn to the physical sciences, Mayr argued that reductionism confuses two kinds of causes: proximate and ultimate.

In Mayr's original (1961) discussion of the proximate–ultimate distinction, he offers an example to illustrate it. He lists four causes of a warbler beginning its migration on a given night: (1) The warbler would starve if it did not migrate. (2) The warbler's species has evolved a particular genetic constitution that causes it to migrate under particular circumstances. (3) The warbler's internal physiology is such that it is induced to migrate when day lengths are short enough. (4) Particular

external conditions arose that caused the warbler to migrate given its internal state. According to Mayr (1961), 1 and 2 are ultimate causes while 3 and 4 are proximate causes.

Along with the example, Mayr explicitly characterizes the proximate–ultimate distinction in four ways in “Cause and Effect in Biology.” First, proximate causes are the purview of “functional biology.” Mayr’s primary example is physiology. Ultimate causes are the purview of evolutionary biology. This division is characterized by the questions each discipline asks, generating Mayr’s second characterization. Proximate causes can be invoked to answer ‘how?’ questions while ultimate causes can be invoked to answer ‘why?’ questions. Third, Mayr claims that the distinction can be made using the notion of a genetic program. Proximate causes concern the operation of the genetic program while ultimate causes explain the origin of the program. Finally, Mayr characterizes ultimate causes as those that “have a history and have been incorporated into the system through many thousands of generations of natural selection” (Mayr 1961). He does not offer a contrasting characterization of proximate causes, but the implication appears to be that ultimate causes are historical in a way that proximate causes are not. Each of these characterizations raises hard interpretive questions, but Mayr’s initial characterization provides the common ground among current researchers and will serve as a starting point.

Tinbergen introduced his four questions in his 1963 paper “On the Aims and Methods of Ethology,” written primarily to honor his friend and mentor, Konrad Lorenz. Tinbergen argues that Lorenz’s preeminent contribution was to show that it is possible to study behavior from a biological perspective, a perspective characterized by a particular set of questions. Following Julian Huxley (1942), Tinbergen divides biological inquiry into three types of questions: (1) Evolutionary questions concern both the historical progression and general mechanisms of evolutionary change. (2) Survival value questions concern a trait’s contribution to fitness. (3) Questions about causation concern both internal mechanisms and external triggers. Tinbergen’s use of the term ‘causation’ is somewhat idiosyncratic, and most biologists now use the term ‘mechanism’ instead. I will follow this convention with the proviso that I use the term in its scientific vernacular sense. I neither assume nor attribute to Tinbergen any particular conception of mechanism developed in recent philosophy of science (e.g. in Machamer et al. 2000). To Huxley’s three questions, Tinbergen adds a fourth concerning development over an organism’s lifetime. We can thus ask of a trait “How did it evolve?”, “How does it contribute to survival?”, “How is it accomplished mechanistically?”, and “How does it develop over the lifetime of the organism?”.

In addition to honoring Lorenz, Tinbergen uses the “Aims and Methods” paper to solidify the identity of the burgeoning field of ethology. In particular, Tinbergen argues for a thorough integration of the biological study of animal behavior across disciplinary boundaries, including psychology, neurophysiology, and evolutionary biology. To this end, he notes that “in speaking of the ‘four problems of biology’ we apply a classification which is pragmatic rather than logical” (Tinbergen 1963, p. 426) and that “a comprehensive, coherent science of ethology has to give equal attention to each of them and to their integration” (Tinbergen 1963, p. 411). Unfortunately, Tinbergen provides little detailed discussion of how this integration should

proceed. One of the central interpretive aims of the paper will be to reconcile an apparent tension between Tinbergen's call for integration and Mayr's case for the autonomy of evolutionary biology.

Disentangling Mayr and Tinbergen

The Standard View, that Mayr's proximate–ultimate distinction parses Tinbergen's questions into mechanistic and developmental questions on the one hand, versus evolutionary and survival value questions on the other, is typically stated without argument (e.g. Sherman 1988; Holekamp and Sherman 1989; Alcock 1993; MacDougall-Shackleton 2011; Bateson and Laland 2013; Nesse 2013; Taborsky 2014; Hofmann et al. 2014). However, the Standard View is not implied by Mayr's and Tinbergen's initial characterizations of their views.¹

In a review of Tinbergen's presentation of the four questions in his 1972 book, *The Animal in its World*, Sara Shettleworth divides Tinbergen's questions differently: “the first three [mechanisms, development, and evolution] have to do with mechanism or, as Tinbergen puts it ‘How is it done?’; and the last [survival value] with function or ‘What is its use?’” (Shettleworth 1974, p. 581). For Shettleworth, Tinbergen's questions do not divide into sets of two; rather, survival value is most naturally categorized as a “why?” question and the other three as “how?” questions. Alternatively, philosophers standardly divide functional explanations into two types, historical and causal role explanations (Godfrey-Smith 1993). The former concern a history of selection that explains *why* a trait exists while the latter concern causal contributions to a disposition or capacity, and thus explain *how* a system works. Questions about survival value concern a trait's causal contribution to an organism's capacity to survive, thus explaining *how* the system works. As Tinbergen himself emphasizes, even if there had been no evolutionary history and animals had been recently created, the question of *how* they manage to survive would be of interest to biologists (Tinbergen 1963; Griffiths 2009). On this manner of parsing, evolutionary questions are ultimate while the other three are proximate. The point is not that either of these alternative classifications is a correct representation of the relationship between the four questions and the proximate–ultimate distinction, but that both appear entirely reasonable given Tinbergen's and Mayr's initial characterizations of their distinctions. The Standard View is not the only interpretive option on the table. According to the interpretation I will defend, the proximate–ultimate distinction does not map cleanly onto any particular way of dividing Tinbergen's questions.

¹ The earliest explicit statement of the Standard View I have found occurs in Sherman (1988) and Holekamp and Sherman (1989). As an anonymous referee has noted, the Standard View appears to be presumed in Wilson's (in)famous “amoeba diagram” in his (1975) *Sociobiology*. It is worth noting the view met with backlash at the time. I suspect the dominance of this interpretation can largely be attributed to John Alcock's (1993) inclusion of it, citing Sherman's and Holekamp's papers, in the first chapter of the fifth and subsequent editions of his influential *Animal Behavior* textbook. As of now, the book is in its eleventh edition (Rubenstein and Alcock 2018). The view is usually stated without argument because it is thought of as established textbook knowledge.

The Standard View is not only not obvious but faces several difficulties. First, it cannot make sense of the uncontroversial link between history and ultimate causes. The standard picture makes the distinction between historical and non-historical a second axis, orthogonal to the proximate–ultimate distinction, dividing Tinbergen’s four questions. Evolution and development are historical while survival value and mechanisms are not. However, Mayr consistently explicates the proximate–ultimate distinction as, at least in part, a matter of ultimate causes being historical in some important sense that proximate causes are not. If the difference between proximate and ultimate causes consists in part in the latter but not the former being historical, then the standard picture cannot be accurate in treating the historical versus non-historical distinction as orthogonal to the proximate–ultimate distinction.

Second, there is little to no textual evidence that Mayr or Tinbergen conceived of the four questions as a simple refinement of the proximate–ultimate distinction. One would expect that if the two frameworks were marking basically the same distinctions, Mayr and Tinbergen would have indicated this. However, neither ever cites the other in the relevant contexts, and it was not because they were not aware of one another’s work. Mayr and Tinbergen were close personal friends, and in one letter, Mayr (1963) thanks Tinbergen for having sent him a copy of “On the Aims and Methods of Ethology” and offers comments on the manuscript. Notably, Mayr says little about the four questions, instead focusing on critiquing Tinbergen’s definitions of innateness and learning. Mayr then writes (p. 2), “I hope I sent you a reprint of my paper on ‘Cause and Effect in Biology,’ in which I have discussed some of the problems touched upon by you.” Mayr and Tinbergen knew each other’s work well yet never suggest in publications or private correspondence that their frameworks are intimately related. Mayr’s claim that Tinbergen’s discussion merely “touched on” some of the same ideas suggests just the opposite. In “Aims and Methods” Tinbergen does use the phrase “proximate cause” when he notes that the crude error of treating a function as a proximate cause is no longer a major problem. He may well be using the terminology in Mayr’s sense, though he does not cite Mayr. However, if Tinbergen is using Mayr’s concept of proximate causation here, it is all the more telling that he does not invoke the concept to explicate his own framework.

That Mayr (1982, 1993) often uses the terms ‘ultimate’ and ‘evolutionary’ interchangeably may be taken to suggest the Standard View. However, though Mayr often uses ‘evolutionary’ as a synonym for ‘ultimate’, he also uses ‘historical’ as a synonym for both. This should give us pause about reading too much into Mayr’s tendency to use other terms as proxies for ‘ultimate’. As I will explain in a later section, he clearly does not think ‘ultimate’ and ‘historical’ are literally synonymous in his proposed usage, so we cannot infer that he takes ‘ultimate’ and ‘evolutionary’ to be synonymous either. I will argue that ultimate causes specifically concern natural selection (see Ariew 2003; Gardner 2013). And, given Mayr’s adaptationist views (see especially Mayr 1988), it is not surprising he would find it natural to treat ‘selection’ and ‘evolution’ as interchangeable. It is also important that Mayr equates evolutionary and ultimate *causes*, but he tends to refrain from calling other evolutionary processes *causes*. I will return to this point in “[Chance and constraint](#)” section. In any case, this linguistic usage pattern lends less support to the Standard View than to the view that only evolutionary questions are ultimate while the other three are proximate.

The most plausible textual case for the Standard View occurs when Mayr approvingly notes that Robert Boyle “understood perfectly well that the explanation of the mechanical workings of a structure is an entirely independent endeavor from the explanation of the reason why the organ exists and what its role in the life of the organism is. Thus he made quite clearly a distinction between proximate and ultimate causations” (Mayr 1988, p. 235). However, this passage only supports the Standard View if we assume that ‘explanations of why the organ exists’ maps neatly onto Tinbergen’s evolutionary questions, and ‘role in the life of the organism’ maps neatly onto Tinbergen’s survival value questions. Neither is obvious, so absent other evidence, this passage offers little support to the Standard View. Given Mayr’s familiarity with Tinbergen’s four questions, as evidenced by correspondence, it is striking that in over four decades of publications addressing the proximate–ultimate distinction (e.g. Mayr 1961, 1974, 1982, 1984, 1988, 1992b, 1993, 1996, 1997, 2004), this is the closest we get to a textually supported connection in Mayr.

The third problem with the Standard View is that it has led to little insight concerning how the proximate–ultimate distinction fits into Mayr’s larger anti-reductionist argument. Simply naming two kinds of causes does not in itself show that one cannot be reduced to the other. Otherwise, reductionism of any sort could be defeated all too easily. Chemistry cannot be reduced to physics because it confuses chemical causes with physical causes. But, Mayr does not simply name the two causes. He links the proximate–ultimate distinction to a complex array of concepts and arguments. A good interpretation of his framework should allow us to reconstruct a reasonably plausible anti-reductionist argument that actually invokes the concepts Mayr himself invokes, for example genetic programs and history. The Standard View simply assimilates Mayr’s distinction to a framework that was developed to emphasize integration rather than autonomy between disciplines, leaving it unclear how Mayr’s distinction could possibly do the philosophical work he introduces it to do.

Integration versus autonomy

Integrating Tinbergen’s four questions requires more than answering each individually. One can pick any four questions about any topic at random, and it would be clear that simply answering each would not constitute an integration of those questions. However, it is not immediately obvious what is required for a successful integration. At the very least, integration appears to require showing how the answers to the different questions dovetail with and constrain one another. This very basic requirement leads immediately to a tension in the standard picture of the relationship between the proximate–ultimate distinction and the four questions.

Autonomy and integration pull in opposite directions. The more two explanations dovetail and constrain one another, the less autonomous they are. While Tinbergen emphasizes the pragmatic nature of his division between the four questions, Mayr emphasizes the distinctness and autonomy of “how?” versus “why?” questions. This alone is not a problem. Constraints that push in opposite directions often provide a useful narrowing of theoretical options. Autonomy comes in degrees; however, it

is no trivial task to distinguish integrating proximate “how?” and ultimate “why?” questions from conflating them.

This tension is at the heart of heated controversies. The proximate–ultimate distinction is regularly invoked in critiques of integrative projects (e.g. Mayr 1984; Sherman 1988; Bolhuis 2005; Scott-Phillips et al. 2011; West et al. 2011; Dickins and Rahman 2012; Fedyk 2015). For example, evolutionary psychology has been criticized on the grounds that hypotheses about proximate causes are taken to be confirmed by speculations about ultimate causes (e.g. Lickliter and Berry 1990; Fedyk 2015). In response, some have advocated rethinking or abandoning the proximate–ultimate distinction because it serves as a conceptual barrier to integrative work (e.g. Jamieson 1989; Francis 1990; Lickliter and Berry 1990; Dewsbury 1994; West-Eberhard 2003; Ariew 2003; Amundson 2005; Thierry 2005; Jablonka and Lamb 2005; Laland et al. 2011; Calcott 2013a, b; Laland et al. 2013a, b; Watt 2000, 2013). Researchers in evo-devo in particular have suggested that Mayr’s distinction carries with it the presumption that development is irrelevant to evolution, thereby precluding the integration of developmental and evolutionary explanations evo-devo seeks to provide. These suggestions are met with vigorous defenses of the distinction, along with accusations that the critics are making fundamental conceptual mistakes (e.g. Sherman 1989; Mayr 1993; Alcock and Sherman 1994; Dickins and Barton 2013; Gardner 2013).

To complicate matters further, the debate has revealed considerable variation in researchers’ conceptions of the proximate–ultimate distinction (Haig 2013; Laland et al. 2013b; Hogan 2015). For example, there is disagreement about whether genetic drift is an ultimate cause. For critics, this is only further evidence that we need to abandon or rethink the proximate–ultimate distinction (e.g. Ariew 2003; Laland et al. 2013b). Ironically, these claims are often made alongside claims that Tinbergen’s framework is superior and should be favored (e.g. Bateson and Laland 2013), but if the Standard View is correct, Tinbergen’s four questions map onto the proximate–ultimate distinction. The four-question framework would thus lead to all the same theoretical puzzles independently. Simply abandoning the labels ‘proximate’ and ‘ultimate’ does not address the underlying problem.

Much recent literature (e.g. Laland et al. 2011; Calcott 2013a, b; Laland et al. 2013a, b; Scholl and Pigliucci 2015) has sought to diagnose the source of “Mayr’s insistence that development is irrelevant to evolution” (Laland et al. 2013b, p. 796). Typically, claims that Mayr took development to be irrelevant to evolution (e.g. Laland et al. 2011; Scholl and Pigliucci 2015) are supported only by citations to two specific critiques of work in evo-devo (namely Mayr 1984, 1992a). Laland et al. cite Ron Amundson (2005) as a historical authority supporting the claim that these two critiques reveal Mayr’s in-principle rejection of the relevance of development to evolution. However, Amundson’s argument is unconvincing.

Amundson (2005) correctly notes that Mayr invokes the proximate–ultimate distinction in critiques of several developmental biologists. However, as Amundson concedes, Mayr’s remarks are aimed at responding to specific critics of the so-called Modern Synthesis of evolutionary biology, genetics, and other biological subfields to which Mayr was a key contributor. Mayr accuses his developmentalists critics of confusing proximate and ultimate causes, and Amundson moves from this to the

claim that Mayr was making an in-principle argument against the relevance of development to evolution. Amundson attempts to justify this logical leap in two ways: First, he notes that Mayr (1992a) makes very general claims about developmentalist critics confusing proximate and ultimate. Second, Amundson (2005, p. 223) argues that “Mayr never gives a hint about how to relate development to evolution without committing the proximate–ultimate fallacy” thus making it “hard to resist the conclusion that Mayr believes that the irrelevance of development to evolution follows directly from the distinction itself.”

However, while it is true that Mayr (1984, 1992a) claims that confusions about proximate and ultimate causes have been rampant in developmental biology, this does not imply or even suggest that development is irrelevant to evolution, only that its relevance has been widely misconstrued. Far from an “insistence that development is irrelevant to evolution,” in the same paper in which Mayr claims some developmentalist critics of the Synthesis have conflated proximate and ultimate causes, Mayr writes that “Those *developmental biologists* who will work on this problem, together with the molecular biologists, *will certainly make a far greater contribution to our understanding of evolution* than those who present to the world a completely erroneous picture of the current beliefs of the Darwinians” (Mayr 1984, p. 1262, my emphasis). In later work, Mayr claims that “No Darwinian will ever question the importance of development in evolution, but evolutionary interpretation is constrained by the extent to which the proximate causations of development have been elucidated by the embryologists” (Mayr 1988, p. 537). Mayr (1988, p. 542) lists the “role of development” as one of the two “frontiers of evolutionary biology likely to see the greatest advances” in coming decades. Mayr’s explicit recognition of the role of development in evolution occurs throughout his (1988) collection of papers on philosophy of biology and positively valenced overviews of work in evo-devo features prominently in his final (2004) book.

That Mayr offers no explicit account of how development contributes to evolution would hardly justify attributing to him the view that development is irrelevant to evolution, and it offers no support at all given Mayr’s explicit avowal of the opposite view as documented above. It is also not true that Mayr never discusses how development can be relevant to evolution (see especially Mayr 1988, 2004). I will provide some positive characterization of his views on this issue in the final section. For now, the important point is that given Mayr’s overt recognition that development is not only relevant but important to evolutionary explanation, interpretations that purport to explain why he held the opposite view must be mistaken (e.g. Laland et al. 2011; Calcott 2013a, b; Scholl and Pigliucci 2015). It is beyond the scope of this paper to critique the details of these interpretations; however, one important point of disagreement concerns whether non-selective evolutionary processes like drift are ultimate causes. I argue that they are not. The opposite view is motivated by the position I aim to undermine, that only ultimate causes can contribute to evolutionary explanations.² In my view, extant interpretations also underplay the importance of

² Both Gardner (2013) and Scholl and Pigliucci (2015) offer important critiques of Laland et al. (2011). Calcott (2013a, b) and Scholl and Pigliucci (2015) characterize drift and other non-selective evolutionary processes as ultimate causes while Ariew (2003) and Gardner (2013) deny that they are.

the concept of genetic programs in Mayr's account. For example, Scholl and Pigliucci (2015) explicitly set this characterization aside as irrelevant.

The remainder of the paper will be focused on developing a positive interpretation of Mayr's proximate–ultimate distinction and its role in Mayr's larger anti-reductionist argument. While I attempt to reconstruct Mayr's position so that it looks plausible given his assumptions, I do not intend what follows as a defense of Mayr's arguments. Though I think Mayr's views are more defensible than they are often given credit for being, the goal here is primarily clarification.

Reduction versus analysis

Mayr draws a distinction between reduction and analysis. The proximate–ultimate distinction serves to show that reduction is impossible, but it is meant to leave open the possibility of analysis. I will argue that Mayr and Tinbergen shared a general conception of integration via analysis, so there is no conflict between Mayr's and Tinbergen's philosophical aims.

Neither Mayr nor Tinbergen provide a detailed account of how to integrate different areas of biological inquiry, but both provide enough discussion to make it clear that they have in mind a general practice that philosophers of science have characterized in some detail under the label 'functional analysis'. The canonical account of this practice among philosophers of science is Robert Cummins' (1975, 1983) account, according to which functional analysis consists in breaking down some capacity or disposition of interest into simpler dispositions or capacities, organized in a particular way. For example, the circulatory system has the capacity to transport materials like oxygen, waste, and hormones to different parts of the body. We can decompose this capacity into several sub-capacities including pumping, directing flow, diffusing materials, and so on. This kind of analysis can be iterated, with the various sub-capacities being analyzed in turn, producing a hierarchy of analyses connecting various levels of description.

Philosophers of science have developed many extensions and refinements of Cummins' basic insight. I do not wish to claim that Mayr or Tinbergen had any of these particular views, including Cummins', in mind.³ Rather, we should remember that Cummins' achievement was to characterize in a precise way an explanatory strategy already well entrenched in scientific practice. Before philosophers began theorizing about functional analysis, Mayr and Tinbergen had been engaging in it for decades, and both were quite capable of describing the explanatory strategy in a general way despite lacking a detailed philosophical account.⁴

³ Interestingly, Mayr (1974, 1988) uses the term 'functional analysis', and Mayr (1992b) cites Cummins (1975), but it is not entirely clear from the context whether the citation is approving, disapproving, or neutral.

⁴ However, we should not underestimate Mayr's awareness of the philosophical literature. Both his citations and his correspondence reveal very active engagement with the philosophy of science community. I suspect that by the end of his life, he did have a well-thought-out account of analysis, but my goal here is not to uncover it.

Mayr tells us that while reduction seeks to explain a system's activities by breaking it down into its most basic components, analysis does not require moving to the most basic level (Mayr 1982, 2004). More importantly, reduction, unlike analysis, ignores a system's organization (1982), which Mayr characterizes as the interaction between components (Mayr 2004). Organization explains the emergence of new characteristics that could not be predicted from knowledge of the isolated components of a system, but analysis provides a middle ground between reductionism and holism (Mayr 1982). Mayr claims that "all problems of biology, particularly those relating to emergence, are ultimately problems of hierarchical organization" (Mayr, 1982, p. 64). Whether or not Mayr would endorse the details of Cummins' account, or any particular later development, they are both describing the same general explanatory practice of breaking a system down hierarchically with a special attention to organization.

Tinbergen, too, endorsed a kind of analysis. Integration between disciplines is achieved through a process whereby "achievements of complex systems are, after a varying number of analytical steps, described in terms of achievements of component systems" (Tinbergen 1963, p. 415). Tinbergen, too, appears to be describing the same explanatory process Cummins' account aims to capture. Tinbergen emphasizes that this explanatory strategy allows us to take different perspectives on the same system:

"The fact that we tend to distinguish sharply between the study of causes and the study of effects is due to what one could call an accident of human perception. We happen to observe behavior more readily than survival, and that is why we start at what really is an arbitrary point in the flow of events. If we could agree to take survival as the starting point of our inquiry, our problem would just be that of causation; we would ask: 'How does the animal — an unstable, 'improbable' system — manage to survive?' Both fields would fuse into one: the study of the causation of survival." (Tinbergen 1963, p. 418)

Tinbergen's view, that the difference between survival value and mechanistic questions is a matter of perspective, is similar to Carl Craver's (2013) perspectival account of the relationship between mechanisms and function, minus Craver's commitment to a broader theory of what mechanisms are. It seems Tinbergen agrees with Craver's basic claim that we can study a single system by viewing it from an inside-out or an outside-in perspective. If we "start with behavior," we can view that behavior as a whole to be broken down into components, or as a component itself to be placed in the broader context of higher-level capacities, especially survival and reproduction.

Mayr would have no objection to this, as long as it does not ignore organization, and he does not take issue with Tinbergen's claims in his commentary on Tinbergen's paper (Mayr 1963). While Mayr emphasizes the autonomy between levels in an analysis, because his primary philosophical aim is combatting reductionism, he also notes that his defense of the autonomy of biology is a first step toward a unification of science (Mayr 1988). And, Mayr (1982, p. 65) claims that "with so many components contributing to the functioning of a biological system, it is for the working scientist a matter of strategy and interest to decide the study of which level would make the greatest contribution toward the full understanding of the system under the present

circumstances.” Thus Mayr, too, appreciates the need for integration and recognizes a need to adopt differing perspectives based on explanatory interests.

There remains the question of how to incorporate development and evolution into the sort of analysis Tinbergen has in mind. Tinbergen claims that the difference between mechanistic and developmental questions is merely the timescale over which we view the system. Similarly, Tinbergen emphasizes that we must make inferences about evolutionary history based on observations about current utility, so survival value and evolutionary questions are also divided, at least in part, by the historical nature of the latter. I doubt that Mayr or Tinbergen had determinate views about this, but it is worth noting that there are at least two possible methods for including this historical dimension. One can include backward and forward-looking perspectives in addition to the outside-in and inside-out perspectives, as Craver (2013) does. The historical dimension is simply another perspective we can take on the system. Philosophical work on the relationship between Cummins-style functional analysis and historical conceptions of function (Wright 1973; Millikan 1984) provide options for developing this line of thought (e.g. Kitcher 1993; Walsh and Ariew 1996; Buller 1998). Another, not necessarily incompatible, strategy would be to include the historical dimension by simply conceiving of the system to be functionally analyzed as temporally extended (Dennett 1995; Davies 2001). For example, we can apply functional analysis to break down the capacity of lineages or populations to change and persist over time into, among other things, the capacities of individuals over the course of entire lifetimes to survive and reproduce.

The Standard View gets something right about Tinbergen’s framework. There is a reason to group survival value with evolution, and development with mechanisms. Starting with behavior, survival value and evolutionary questions both concern behavior’s contribution to a larger process, while developmental and mechanistic questions typically require breaking behavior down, especially if we conceive of behaviors as patterns exhibited over a lifetime, rather than as isolated events that occur at the end of a developmental process. Additionally, Tinbergen claims that timescale separates developmental from mechanistic questions and emphasizes the historical character of evolution as opposed to survival value. Thus, the two axes separating Tinbergen’s questions according to the Standard View are supported by the text. The Standard View errs in representing one of the axes as the proximate–ultimate distinction.

The distinction between reduction and analysis allows Mayr to invoke the proximate–ultimate distinction in an argument against reduction without denying that proximate causes can contribute to our understanding of evolution via analysis. After reconstructing Mayr’s anti-reductionist argument, I will return to how analysis allows for evolutionary explanations to include more than ultimate causes.

Teleology and programs

Mayr (1982) distinguishes two types of reductionism. *Explanatory* reductionism says that to understand a system one must break it down into its smallest components. The distinction between reduction and analysis appears to be enough to show

where this kind of reduction goes wrong. It ignores organization. However, Mayr makes a separate case against what he calls *theory* reductionism, the view that the theories and laws of one science are a special case of theories and laws of another (Mayr 1982). He claims that theory reduction “confuses processes and concepts” (Mayr 1982). However, this point about concepts is not specific to evolutionary biology. Mayr claims meiosis is a chemical *process*, but nevertheless a biological *concept* that cannot be reduced to physico-chemical concepts. This broad point shows that biology, in general, cannot be reduced to the physical sciences. To make his case against explanatory reductionism of evolutionary biology to molecular biology in particular, Mayr needs a more specific argument. The proximate–ultimate distinction serves to mark the conceptual divide that prevents evolutionary biology from being a subdomain of molecular biology.

In “Cause and Effect in Biology,” one of Mayr’s characterizations of the proximate–ultimate distinction says that proximate causes are invoked to answer “how?” questions while ultimate causes are invoked to answer “why?” questions. Mayr’s point is not that a linguistic distinction marks the biological one. We can use the word ‘how’ to ask about ultimate causes as in ‘How did long necks contribute to the reproductive success of sauropod dinosaurs such that natural selection favored them?’. We can also use ‘why’ to ask about proximate causes. A little context setting will help set up the correct reading. Consider the question ‘Why does the moon move a little farther from the earth each year?’. One might take this question to be asking for a reason, perhaps God’s reason, for moving the moon thusly, but the question can also serve to elicit a causal-mechanistic explanation for the moon’s movement away from the earth. Now, consider the parallel question ‘Why does the heart beat faster when there is caffeine in the system?’. This could call for an answer in terms of selection, but the more natural reading is that it simply asks for the physiological mechanisms that explain the heart’s reaction to the presence of caffeine.

For Mayr, ‘how?’ versus ‘why?’ serves as an imperfect marker of the distinction between causes on the one hand and reasons or ends on the other. According to Mayr, “The clear recognition of two types of causation in organisms has helped to solve an important problem in biology, the problem of teleology” (Mayr 1988, p. 3). A hallmark of the scientific revolution was the rejection of ancient and medieval applications of teleological reasoning to the cosmos. In slogan form, physics progressed when it came to focus on causes rather than purposes. Biology, on the other hand, and evolutionary biology in particular, appears to require reasoning about what a given trait is for, or what good it does for the organism. Biological explanation appears to be ineliminably teleological, but according to dominant conceptions of scientific reasoning, teleological reasoning is unscientific. There are three possible responses to this: (1) claim that biological explanation is not really teleological, (2) admit that biological explanation is not really scientific, or (3) claim that teleological reasoning can be scientific after all. Philosophers and scientists have tried all three, but Mayr argues that the class of processes that have been labeled as teleological are not unified and a combination of all three strategies is necessary.

Mayr distinguishes four phenomena that have all traditionally been grouped under the heading of teleology (Mayr 1974, 1982, 1988, 1992b, 2004). (1) *Teleomatic* processes simply converge on an end as a result of natural laws. Mayr’s

primary examples are the operations of gravity and the second law of thermodynamics. (2) *Teleonomic* processes are controlled by a computational program. Mayr includes developmental and cognitive processes in this group, along with the operations of digital computers. (3) *Cosmic teleology* is the kind of teleological process that science has eschewed. It would involve some sort of fundamental end-directedness in the universe. According to Mayr, cosmic teleology does not exist, teleomatic processes are not really teleological because they have no true goal, and teleonomic processes are scientifically respectable because the theory of computation has shown us how that kind of teleology is explicable mechanistically.

Mayr's fourth category is the process of adaptation through natural selection. Natural selection occupies a place between teleomatic and teleonomic processes. On the one hand, like teleomatic processes, natural selection has no goal and is not the result of a program. But, like teleonomic processes, adaptation through natural selection licenses, or even requires, explanations relying on teleological language and reasoning. It is "an optimization process, but one of a very special kind. It is neither teleologically programmed nor controlled by any law, but is entirely opportunistic" (Mayr 1988, p. 105). Because natural selection is a process whereby a *contribution to* reproductive success explains the proliferation of a trait in a population, we can explain a trait's frequency in the population by treating reproductive success as an *end* and asking by what means it is achieved. For Mayr, natural selection is "teleological" (scare quotes because his entire point is that the blanket term 'teleological' is misleading) enough to block reduction to the physical sciences, but not so teleological that it is unscientific (Smocovitis 1992).

Despite his claim that the proximate–ultimate distinction helps solve the problem of teleology, and his regular juxtaposition of the two issues (e.g. Mayr 1961, 1974, 1984, 1988, 1992b, 2004), Mayr is not explicit about their connection. The gap can be filled by his concept of a program, which occurs both in his characterization of the proximate–ultimate distinction and in his delineation of the two legitimate types of "teleology" in biology (see the post-script in Mayr 1988, essay 3). Recall that Mayr characterizes proximate causes as those that govern the operation of a genetic program. Teleonomic processes are defined as those controlled by a program. Therefore, proximate causes are those invoked in the operation of one kind of teleonomic process. The proximate causes of a warbler's migration include both the inputs, in the form of external environmental conditions, and internal implementation of the program governing the migratory behavior. The migratory behavior is a teleonomic process.

Though Mayr (1988, p. 60) calls teleonomic processes "strictly causal and mechanistic," he also says that "teleonomic and adaptational phenomena have a history and cannot be explained *directly* through a strictly causal-mechanical explanation" (Mayr 1988, p. 59, my emphasis). This claim requires explanation, since it appears Mayr is not only contradicting himself but is also blurring the proximate–ultimate distinction by associating teleonomy, and by extension proximate causes, with history. Recall that in Mayr's original (1961) discussion, it is ultimate causes that "have a history."

Mayr (1974, 1982, 1988) explicitly denies that programs are defined historically, but there remains the question of how programs are generated. In principle,

a program could arise by chance, but this would be vanishingly unlikely. Programs can also create other programs, but this leaves open the question of where the original program came from. According to Mayr, Darwin solved this problem by showing how to mechanistically generate a program from a process that is not itself teleonomic, namely natural selection (see especially Mayr 1982, 1988). “Having a history” means “having a history of selection.” Mayr characterizes ultimate causes those that explain the evolutionary origin of a program. Thus, ultimate causes are those that contribute to a history of natural selection.

All traits favored by natural selection are favored because they contribute to reproductive success, so the question facing an evolutionary biologist is really what “end” does a given trait serve that is itself a means of achieving reproductive success. The ultimate cause of a warbler’s migration is that it prevents it from starving, which in turn contributes to its reproductive success.⁵

Proximate and ultimate causes correspond to two of the scientifically legitimate forms of “teleological” process. Proximate causes explain the operation of teleonomic processes, whereas ultimate causes are cited in explanations of adaptation through natural selection. However, this leaves us with two remaining puzzles: (1) In what sense do proximate causes answer “how?” rather than “why?” questions, and vice versa for ultimate causes, if *both* kinds of causes are associated with “teleological” processes? (2) How does this division between causes that contribute to two kinds of “teleological” explanation establish the irreducibility of evolutionary biology to molecular biology and other fields? These questions can be answered by looking more closely at the Mayr’s conception of historical explanation, and its relation to the proximate–ultimate distinction.

Historical narrative

In “Cause and Effect in Biology,” Mayr (1961) notes that teleological “why?” questions can be interpreted as “what for?” or as “how come?” questions. He claims that evolutionary biologists always have in mind the “how come?” question, so it appears that Mayr’s view is that the apparently teleological questions in evolutionary biology are equivalent to questions about historical origins. Many authors still emphasize this part of Mayr’s formulation of the proximate–ultimate distinction (Laland et al. 2013a; Haig 2013). However, in his 1982 *Growth of Biological Thought*, Mayr explicitly reverses his position on this characterization. “The question ‘why?’ in the sense of ‘what for?’ is meaningless in the world of inanimate objects. One can ask, ‘Why is the sun hot?’ but only in the sense of ‘how come?’ By contrast, in the living

⁵ In the second of Mayr’s four examples at the beginning of “[Overview of the two frameworks](#)” section, Mayr (1961) seems to suggest that the *possession* of a genetic constitution favored by selection is an ultimate cause. He repeats this example, substantially reworded, in a later book (Mayr 1984), explicitly noting that the relevant evolutionary process is selection. However, he still appears to be saying that the genetic program that *results* from that process is an ultimate cause. Since the example is anomalous in this respect, and originates in his earliest work on the distinction, I am inclined to think it can be dismissed as Mayr being uncaredful and conflating process with product.

world the question ‘what for?’ has powerful heuristic value” (Mayr 1982, p. 72). Mayr’s claim that “‘what for?’ questions have heuristic value, should not be taken to suggest that Mayr saw them as eliminable. Sometimes heuristics are necessary to make a question tractable.

Mayr refined his view because he recognized that evolutionary biology is not the only science concerned with historical origin questions. As he notes in that same work, embryology, geology, and astronomy all provide historical “‘how come?’” explanations. He embraces that evolutionary biology asks “‘what for?’” questions and rejects the view that they can be straightforwardly translated into nothing more than “‘how come?’” questions (see also Mayr 1974). However, Mayr continues to emphasize that ultimate causes are historical, even using ‘historical’ as a proxy term for ‘ultimate’. Mayr recognized that simply pointing out that evolutionary biology is a historical science would not suffice to block reductionism, but he did not change his mind that historicity somehow sets the search for ultimate causes apart.

Evolutionary biologists typically aim to explain events that are in the past and extend over long timescales relative to human life spans, but (contra Ariew 2003) neither of these features define Mayr’s conception of historical explanation. When Mayr says that explanations citing ultimate causes are historical, he means that they take the form of narratives (Mayr 1982, 2004). This focus on narratives groups evolutionary biology with the humanities (“Geisteswissenschaften”) as opposed to the “exact sciences” and “functional biology”, which are instead concerned with formulating laws (Mayr 2004).

Still, there remains the puzzle of how narrative explanations set evolutionary biology apart. Given that, as Mayr explicitly recognizes, other sciences including embryology, astronomy, and geology also make use of historical narrative, it is not immediately clear how appealing to narratives helps Mayr’s case against reductionism. This puzzle can be solved with the help of a useful distinction Currie (2014) has drawn between simple and complex narratives. Simple narratives are applications of a general mechanism or law to a particular case. Currie’s primary example is the snowball earth theory, according to which glaciation increased Earth’s albedo (its tendency to reflect solar radiation back out into space) sufficiently to create a positive feedback loop, resulting in runaway cooling and eventually glaciation of the Earth’s entire surface. This narrative applies a general mechanism, albedo’s effect on climate, to a specific case.

A complex narrative is not unified by a particular general mechanism. Currie notes that complex narratives rely on a specific, diffuse, and complex set of disparate mechanisms working in concert. Currie’s primary example here is, tellingly, a biological one: sauropod gigantism. Paleontologists’ explanation for why sauropod dinosaurs reached such large sizes compared to any other land animals in history relies on a complex array of mechanisms and specific, historically contingent events. The point is not that no general mechanisms or laws are invoked, but that, as Currie puts it, “in a complex narrative, we appeal to regularities in order to support specific factors in the narrative—it is the narrative which carries the ‘explanatory load’. In simple narratives, the general model plays a unifying role, and it is the regularity which carries the explanatory load” (Currie 2014, p. 1169).

Narratives are not specific to evolutionary biology. However, Mayr emphasizes that the targets for narrative explanation in evolutionary biology are especially unique and complex (Mayr 1961, 1982, 1988, 2004).⁶ Mayr claims that attempts to capture historical narratives in evolutionary biology “in terms of covering laws fail to convince” (Mayr 1982, p. 72) and that “phenomena that are due to a chain of historical events cannot be ascribed to simple laws and can therefore not be proven in the same way as phenomena studied in the physical sciences” (Mayr 1988, p. 254).

This is a plausible difference between the kind of historical explanation that occurs in evolutionary biology and the kind that occurs in geology and astronomy. Currie suggests that there is a tension between reductive explanation and complex narratives because complex narratives emphasize complex interactions between contingent causal factors rather than subsumption under general laws. Mayr agrees. Note that Mayr, too, contrasts the complexity and uniqueness of historical narrative with a search for laws. Mayr does not extend this point to the narratives used in the physical sciences because the components of those systems are all alike.

“...uniqueness in the inanimate world is limited to complex systems, while the basic building blocks of these systems (elementary particles, atoms, molecules and crystals) consist of identical components. In the living world, uniqueness is seen even at the molecular level in the form of DNA or RNA.” (Mayr 1988, p. 16)

Mayr believes that the underlying uniformity of planets, stars, weather, systems, and mountains allows their activities to be subsumed under general laws in the form of simple narratives (though of course Mayr lacked that terminology).

It is more difficult to apply the distinction between simple and complex narratives to capture the difference between evolutionary biology and, say, embryology. I suspect Mayr has in mind the following: In embryology and other areas of non-evolutionary biology that engage in historical narrative, the notion of a program allows for simple narratives. Recall that Mayr contrasts the “entirely opportunistic” character of natural selection with being governed by a law *or program* (Mayr 1988, p. 105). Mayr need not, and does not, claim that development is a simple process. Mayr recognizes that developmental histories are unique and complex (see Mayr (1988), essay 3 postscript), but unlike evolution, where the target of explanation is often a particular historical event, developmental biologists seldom seek to explain some specific, individual developmental outcome. Rather, developmental biologists seek to explain developmental patterns, including *patterns* of variation. Those developmental outcomes must be repeatable across individuals and generations, at least approximately. These end-directed patterns are explained, according to Mayr,

⁶ This claim and the earlier division between the role of narrative in delineating the humanities from the exact sciences echoes the views of neo-Kantians whose work Mayr would likely have encountered, especially Heinrich Rickert (see Staite (2013)). However, I have been unable to find explicit reference to the neo-Kantians in Mayr’s work. It is worth noting that Mayr often cites Kant himself approvingly (see especially Mayr (1982, 1988)).

by the operation of a program, and thereby subsumed under a general rule or simple narrative.

Whether development can really be characterized by the unfolding of a program is controversial (Ariew 2003; Oyama 2000). Mayr himself abandons the notion that a specifically genetic program will do the theoretical work he requires of it and introduces the concept of a “somatic program” to capture non-genetic mechanisms of development (Mayr 1988). I believe Mayr’s notion of a program is more defensible than it is often taken to be; however, I will not attempt to defend it. My goal here is not to defend Mayr’s argument, but to show how the proximate–ultimate distinction fits into a coherent, *prima facie* defensible total argument for the autonomy of evolutionary biology given Mayr’s other well-documented views.

Invoking a program allows for an explanation that looks like the explanations given in the physical sciences, because we can provide something like a general mechanical rule governing the process. This is why Mayr paradoxically associates proximate causes, which contribute to the true end-directedness of teleonomic processes, with “how?” questions. The more overtly teleological “why?” questions he associates with ultimate causes, because they are essential for actually constructing complex narratives and cannot be replaced by any actually informative general mechanical rule. Of course, in every given case the narrative will invoke only mechanical processes, but Mayr thinks evolutionary narratives will be too contingent, complex, and unique to share much beyond the “end” of reproductive success. Since no law or program can capture the process of selection, adaptation is not a special case of a teleomatic or teleonomic process. Evolutionary biology thus cannot be reduced to, say, molecular biology.

Chance and constraint

It is now possible to say more explicitly how the Standard View is too simple. As Tinbergen (1963) argues, information about survival value is useful for constructing historical narratives, but even if organisms had just been created by a powerful deity, we would still want to know how they manage to survive (see also Griffiths 2009). And, that a trait contributes to survival in a particular way currently does not imply immediately that selection is or was at work. As Tinbergen (1963) notes, we need more information to make this inference. On Mayr’s view, a trait’s contribution to survival value only counts as an ultimate cause if that contribution is part of a narrative explanation involving actual selection. This does not imply that ultimate causes can only explain a trait’s origins. A narrative about recent maintenance of the trait or about probable future evolution are also about actual selection. This point also reveals a flaw in several critics’ claim that Mayr’s concept of ultimate causation treats functions as causes (Francis 1990; Ariew 2003; Bolhuis 2005). Mayr recognizes as ultimate causes only those contributions to reproductive success that occur in a causally explanatory narrative invoking actual selection (see Mayr (1988), essay 3, footnote 1).

Similarly, not every cause cited in a historical narrative of a trait’s evolution counts as ultimate. Natural selection, Mayr emphasizes, is a two-step process. The

first step is variation, and the second, he calls “selection proper” (Mayr 1988, 1997). While Mayr argues that it is essential to understand the origins of variation to fully understand the evolution of a trait, only “selection proper” is an ultimate cause. Selection can only exert an influence within the bounds of available variation, so it can be as important to explain why variation is lacking as why it is present. “Directional causes are caused by natural selection, but constrained by the potential of the existing genotype” (Mayr 1988, p. 109). Under the heading of constraints, Mayr includes phenotypic plasticity (presumably including developmental, cognitive, physiological, and behavioral plasticity), lack of variation, developmental canalization, “evolutionary noise” (I suspect he has drift and repeated mutation in mind here), cohesion of the genotype and developmental system, and limited potential of a particular body plan (*bauplan*) (Mayr 1988).

Explanations of variation, or lack thereof, can take two forms. First, some invoke chance. Chance in this context does not refer to fundamental randomness; rather, it means randomness with respect to effects on fitness. Change due to drift or mutation, or persistence due to lack of variation that might have but did not occur, can only lead to fitness increases by accident. Therefore, they are not “teleological” and thus are not ultimate causes. Nor are they proximate causes, because chance is not a cause at all. The second form of explanation consists in analysis of the individual level processes that give rise to variation at the population level. This kind of analysis can invoke proximate causes and lower level laws. This includes invoking goal-directed, teleonomic developmental, behavioral, and physiological processes. However, it is important not to conflate the ultimate cause for the teleonomic process itself with the goal of that process, as early work on the evolution of altruism often conflated the selective advantage of altruistic behavior with the proximate psychological motives for that behavior. Teleonomic processes are “teleological,” but it is a teleology constituted by the operation of a program not by the operation of natural selection in a complex historical narrative, so they also are not ultimate causes, *even if they are relevant to evolution*.

If Mayr had taken every cause relevant to the historical process of evolution to be ultimate, then the category of ultimate causes would expand beyond any usefulness (Gardner 2013). As Williams (1966) notes, gravity is sufficient to explain why flying fish fall back into the water. However, gravity is not an ultimate cause, nor are the appearance of mountain ranges, climate shifts, or developmental processes. Mayr isolates selection among the causes relevant to evolution as ultimate because selection exhibits the combination of “teleology” and historicity required for his anti-reductionist argument. But, as Mayr fully recognized, selective advantages are not all that matter to answering evolutionary questions.

Conclusions

I have argued that the Standard View, that Tinbergen’s four questions are a simple refinement of Mayr’s distinction between “how?” and “why?” questions, is mistaken. In its place, I have defended an interpretation according to which Tinbergen and Mayr share a similar vision of integration akin to Cummins’ (1975) account of

functional analysis, though they emphasize different distinctions to serve different ends. Tinbergen emphasizes the merely pragmatic nature of taking different perspectives on the same causal system and urges integration through recognition that the targets of explanation in one domain are the tools of explanation in another. Mayr emphasizes that the role of natural selection in complex narratives licenses teleological reasoning that cannot be captured by the conceptual tools of the physical sciences or “functional biology.” It is no part of Mayr’s account that only ultimate causes are relevant to evolutionary explanations or that all contributions to reproductive success are ultimate causes.

One of the primary motivations for this historical work is to clarify the role of the proximate–ultimate distinction in current debates. Though tracing out the implications in detail is beyond the scope of this paper, I would like to briefly return to the question of why Mayr (1984, 1992a) claims that some of his critics in evo-devo have confused proximate and ultimate causes.

My interpretation suggests that the main point of contention is not whether development is relevant to evolution. I believe that Mayr’s primary objection was to the claim that developmental processes constitute an alternative to natural selection as a fundamental cause of directional adaptive change. By directional, I meant the opposite of random in Mayr’s sense, that is, non-accidentally fitness conducive. If evolutionary change is directional, then it is “teleological,” so it is either the result of selection or the result of a teleonomic program that is itself a result of selection (or the program is the result of another program that is itself a result of selection, etc.). Thus, explanation is incomplete until an ultimate cause is identified. Otherwise, in Mayr’s view, we are forced to posit inherent end-directedness or cosmic teleology.⁷ Accepting Mayr’s four-way distinction between kinds of “teleology,” his structuralist critics claim that development is an alternative direction giving force to selection and deny that it is indirectly explained by selection via the concept of a program, so the remaining scientifically legitimate option left on the table would be to paint developmental processes as teleomatic, or governed by a natural law. As a matter of fact, much of the debate surrounding the import of evo-devo has focused on the role of “laws of form” (Amundson 2005; Medina 2010). I suspect the crux of the debate concerns the cogency and import of laws of form and self-organizational principles in explaining directional change independent of selection.

For Mayr, laws of form are shared developmental programs. And, these programs are historically contingent results of natural selection, plus the manifestation of more basic physical laws and chance. Thus, invoking them as an alternative explanation to selection constitutes a conflation of proximate and ultimate causes. If Mayr is right, then development remains important to evolution, because it helps explain the variation available to selection, but the story is incomplete until we inquire into the origin

⁷ Mayr’s impression that his developmentalist critics were resurrecting a discredited kind of teleology was further encouraged by the tendency of those critics to label their views Lamarckian (e.g. Ho and Saunders 1984). Laurent Loison (2018) has recently, and I think convincingly, argued that Lamarckism, properly understood, indeed carries the supposition that there is an inherently end-directed vital force in living matter.

of the developmental constraints themselves. The process only terminates when we have reached selective processes acting on variation that is entirely explained by chance and mechanical laws. Otherwise, we are injecting inherent end-directedness somewhere. If the critics are right, the further inquiry is pointless because the laws of form are themselves fundamental, and the task is to either defend inherent end-directedness in the universe or explain what mechanical law or process other than selection could produce directional laws of form.

Acknowledgements Work on this paper was spread over time spent in the departments of philosophy at Cornell University, Virginia Commonwealth University, and Colgate University, and I would like to thank all three for their support. Special thanks go to Richard Boyd, Derk Pereboom, William Starr, Frances Fairbairn, Nicole Lee, Annaliese Beery, Maureen O'Malley and two anonymous reviewers, all of whom read drafts at various stages of development and provided helpful commentary. The paper also benefited from useful discussions with Darragh Hare, Hudson Kern Reeve, and audiences in the Cornell Sage School of Philosophy, Cornell Neurobiology and Behavior Department, and the 2017 International Society for the History, Philosophy, and Social Studies of Biology. Finally, I wish to dedicate this paper to the memory of Ann Johnson, who provided encouragement and feedback on this and other work.

References

- Alcock J (1993) *Animal behavior: an evolutionary approach*, 5th edn. Sinauer, Sunderland
- Alcock J, Sherman P (1994) The utility of the proximate–ultimate dichotomy in ethology. *Ethol* 96:58–62
- Amundson R (2005) *The changing role of the embryo in evolutionary thought: roots of evo devo*. Cambridge University Press, Cambridge
- Ariew A (2003) Ernst Mayr's 'ultimate/proximate' distinction reconsidered and reconstructed. *Biol Philos* 18:552–565
- Ariew A, Walsh DM (1996) A taxonomy of functions. *Can J Philos* 26:493–514
- Bateson P, Laland K (2013) Tinbergen's four questions: an appreciation and an update. *Trends Ecol Evol* 28:712–718
- Beatty J (1994) The proximate/ultimate distinction in the multiple careers of Ernst Mayr. *Biol Philos* 9:333–356
- Bolhuis J (2005) Function and mechanism in neuroecology: looking for clues. *Anim Biol* 55:457–490
- Buller DJ (1998) Etiological theories of function: a geographical survey. *Biol Philos* 13:505–527
- Calcott B (2013a) Why the proximate–ultimate distinction is misleading, and why it matters for understanding the evolution of cooperation. In: Sterelny K, Joyce R, Calcott B, Fraser B (eds) *Cooperation and its evolution*. MIT Press, Cambridge, pp 249–264
- Calcott B (2013b) Why how and why aren't enough: more problems with Mayr's proximate–ultimate distinction. *Biol Philos* 28:767–780
- Craver CF (2013) Functions and mechanisms: a perspectivalist view. In: Huneman P (ed) *Functions: selection and mechanisms*. Springer, Dordrecht, pp 133–158
- Cummins R (1975) Functional analysis. *J Philos* 72:741–765
- Cummins R (1983) *The nature of psychological explanation*. MIT Press, Cambridge
- Curie AM (2014) Narratives, mechanisms, and progress in historical science. *Synthese* 191:1163–1183
- Davies PS (2001) *Norms of nature: naturalism and the nature of functions*. MIT Press, Cambridge
- Dennett DC (1995) *Darwin's dangerous idea: evolution and the meanings of life*. Simon & Schuster, New York
- Dewsbury D (1994) On the utility of the proximate–ultimate distinction in the study of animal behavior. *Ethol* 96:63–68
- Dewsbury D (1999) The proximate and the ultimate: past, present, and future. *Behav Process* 46:189–199
- Dickins TE, Barton RA (2013) Reciprocal causation and the proximate–ultimate distinction. *Biol Philos* 28:747–756
- Dickins TE, Rahman Q (2012) The extended evolutionary synthesis and the role of soft inheritance in evolution. *Pros R Soc B* 279:2913–2921

- Fedyk M (2015) How (not) to bring psychology and biology together. *Philos Stud* 172:949–967
- Francis RC (1990) Causes, proximate and ultimate. *Biol Philos* 5:401–415
- Gardner A (2013) Ultimate explanations concern the adaptive rationale for organism design. *Biol Philos* 28:787–791
- Godfrey-Smith P (1993) Functions: consensus without unity. *Pac Philos Q* 74:196–208
- Griffiths PE (2009) In what sense does ‘nothing make sense except in the light of evolution’? *Acta Biotheor* 57:11–32
- Haig D (2013) Proximate and ultimate causes: How come? and what for? *Biol Philos* 28:781–786
- Ho MW, Saunders PT (1984) *Beyond neo-Darwinism: an introduction to the new evolutionary paradigm*. Academic Press, London
- Hofmann HA, Beery AK, Blumstein DT, Couzin ID, Earley RL, Hayes LD, Hurd PL, Lacey EA, Phelps SM, Solomon NG, Taborsky M, Young LJ, Rubenstein DR (2014) An evolutionary framework for studying mechanisms of social behavior. *Trends Ecol Evol* 29:581–589
- Hogan JA (2015) A framework for the study of behavior. *Behav Process* 117:105–113
- Holekamp KE, Sherman PW (1989) Why male ground squirrels disperse. *Am Sci* 77:232–289
- Huxley J (1942) *Evolution: the modern synthesis*. Allen & Unwin, London
- Jablonka E, Lamb MJ (2005) *Evolution in four dimensions*. MIT Press, Cambridge
- Jamieson IG (1989) Levels of analysis or analyses at the same level. *Anim Behav* 37:696–697
- Kitcher P (1993) Function and design. *Midwest Stud Philos* 18:379–397
- Laland KN, Sterelny K, Odling-Smee J, Hoppitt W, Uller T (2011) Cause and effect in biology revisited: is Mayr’s proximate–ultimate dichotomy still useful? *Science* 334:1512–1516
- Laland KN, Odling-Smee J, Hoppitt W, Uller T (2013a) More on how and why: cause and effect in biology revisited. *Biol Philos* 28:719–745
- Laland KN, Odling-Smee J, Hoppitt W, Uller T (2013b) More on how and why: a response to commentaries. *Biol Philos* 28:793–810
- Lickliter R, Berry TD (1990) The phylogeny fallacy: developmental psychology’s misapplication of evolutionary theory. *Dev Rev* 10:348–364
- Loison L (2018) Lamarckism and epigenetic inheritance: a clarification. *Biol Philos* 33:29
- MacDougall-Shackleton SA (2011) The levels of analysis revisited. *Philos Trans R Soc B* 366:2076–2085
- Machamer P, Darden L, Craver C (2000) Thinking about mechanisms. *Philos Sci* 67:1–25
- Mayr E (1961) Cause and effect in biology. *Science* 134:1501–1506
- Mayr E (1963) Mayr’s typed letter to Niko Tinbergen, June 6, 1963. Box 1, Folder “Tinbergen, Niko. 1960–1964” HUGFP 14.17 Papers of Ernst Mayr, 1931–1993. Harvard University Archives, Pusey Library—Harvard Yard, Cambridge, MA. Accessed 3 March 2017
- Mayr E (1974) Teleological and teleonomic: a new analysis. *Boston Stud Philos Sci* 14:91–117
- Mayr E (1982) *The growth of biological thought: diversity, evolution, and inheritance*. Harvard University Press, Cambridge
- Mayr E (1984) The triumph of the evolutionary synthesis. *Times Lit Suppl* 4257:1261–1262
- Mayr E (1988) *Toward a new philosophy of biology: observations of an evolutionist*. Harvard University Press, Cambridge
- Mayr E (1992a) Controversies in retrospect. *Evol Biol* 8:1–34
- Mayr E (1992b) The idea of teleology. *J Hist Ideas* 53:117–135
- Mayr E (1993) Proximate and ultimate causations. *Biol Philos* 8:93–94
- Mayr E (1994) Response to John Beatty. *Biol Philos* 9:357–358
- Mayr E (1996) The autonomy of biology: the position of biology among the sciences. *Q Rev Biol* 71:97–106
- Mayr E (1997) *This is biology: the science of the living world*. Harvard University Press, Cambridge
- Mayr E (2004) *What makes biology unique: considerations of the autonomy of a scientific discipline*. Harvard University Press, Cambridge
- Medina ML (2010) Two “EvoDevos”. *Biol Theory* 5:7–11
- Millikan RG (1984) *Language, thought, and other biological categories: new foundations for realism*. MIT Press, Cambridge
- Nesse RM (2013) Tinbergen’s four questions, organized: a response to Bateson and Laland. *Trends Ecol Evol* 28:681–682
- Oyama S (2000) *The ontogeny of information: developmental systems and evolution*. Cambridge University Press, Cambridge
- Rubenstein D, Alcock J (2018) *Animal behavior*, 11th edn. Sinauer, Sunderland

- Scholl R, Pigliucci M (2015) The proximate–ultimate distinction and evolutionary developmental biology: causal irrelevance versus explanatory abstraction. *Biol Philos* 30:653–670
- Scott-Phillips TC, Dickins TE, West SA (2011) Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspect Psychol Sci* 6:38–47
- Sherman PW (1988) The levels of analysis. *Anim Behav* 36:616–619
- Sherman PW (1989) The clitoris debate and the levels of analysis. *Anim Behav* 37:697–698
- Shettleworth SJ (1974) Function, causation, evolution, and development of behavior: a review of the animal in its world, by N. Tinbergen. *J Exp Anal Behav* 22:581–590
- Smocovitis VB (1992) Unifying biology: the evolutionary synthesis and evolutionary biology. *J Hist Biol* 25:1–65
- Staiti A (2013) Heinrich Rickert. The Stanford encyclopedia of philosophy (Winter 2013 Edition), Zalta EN (ed), <https://plato.stanford.edu/archives/win2013/entries/heinrich-rickert>. Accessed 25 Nov 2019
- Taborsky M (2014) Tribute to Tinbergen: the four problems of biology. a critical appraisal. *Ethol* 120:224–227
- Thierry B (2005) Integrating proximate and ultimate causation: just one more go! *Curr Sci* 89:1180–1183
- Tinbergen N (1963) On the aims and methods of ethology. *Z Tierpsychol* 20:410–433
- Tinbergen N (1972) *The animal in its world: explorations of an ethologist, 1932–1972: field studies*, vol 1. Harvard University Press, Cambridge
- Watt WB (2000) Avoiding paradigm-based limits to knowledge of evolution. *Evol Biol* 32:73–96
- Watt WB (2013) Causal mechanisms of evolution and the capacity for niche construction. *Biol Philos* 28:757–766
- West SA, Mouden CE, Gardner A (2011) Sixteen misconceptions about the evolution of cooperation in humans. *Evol Hum Behav* 32:231–262
- West-Eberhard MJ (2003) *Developmental plasticity and evolution*. Oxford University Press, Oxford
- Williams GC (1966) *Adaptation and natural selection*. Princeton University Press, Princeton
- Wilson EO (1975) *Sociobiology: the new synthesis*. Harvard University Press, Cambridge
- Wright L (1973) Functions. *Philos Rev* 82:139–168

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.