The Debate over Proximate and Ultimate Causation in Biology

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Abstract

It has been over 60 years since Ernst Mayr famously argued for the distinction between proximate and ultimate causes in biology. In the following decades, Mayr's proximate-ultimate distinction was well received within evolutionary biology and widely regarded as a major contribution to the philosophy of biology. Despite its enormous influence, there has been a persistent controversy on the distinction. It has been argued that the distinction is untenable. In addition, there have been complaints about the pragmatic value of the distinction in biological research. Some even suggest that the distinction should better be abandoned. In contrast, Mayr had consistently maintained the significance of the proximate-ultimate distinction in biology. There are also other attempts to defend the distinction. The paper examines the debate by taking an integrated History and Philosophy of Science (HPS) approach and argues for a functional approach to causal concepts in scientific practice.

1. Introduction

It has been over 60 years since Ernst Mayr argued for the distinction between proximate and ultimate causes in biology in his lecture 'Cause and Effect in Biology' in the Hayden Colloquium at the Massachusetts Institute of Technology (MIT).[1] In the following decades, Mayr's proximate-ultimate distinction became 'a hallmark of sociobiology and behavioral ecology, and more broadly, the adaptationist framework within evolutionary biology' (Francis 1990, 401) and 'is justly considered a major contribution to philosophy of biology' (Beatty 1994, 333).[2] Despite its enormous influence, there has been a persistent controversy on the distinction. It has been argued that the distinction is untenable. In particular, the notion of ultimate cause has been challenged (e.g. Francis 1990; Haig 2013). In addition, there have been more complaints about the pragmatic value of the distinction in biological research (e.g. Laland et al. 2011; Calcott 2013; Sterelny 2013). Some (e.g. Laland et al. 2011) even suggest that the distinction should better be abandoned and replaced. In contrast, Mayr (1993; 1994) had consistently maintained the significance of the proximate-ultimate distinction in biology. There are also other attempts to defend the distinction(e.g. Ariew 2003; Scholl and Pigliucci 2015; Dickins and Barton 2013; Vromen 2017; Conley 2020; Ramsey and Aaby 2022)

[1] The lecture took place on 1 February 1961. It was adapted to an article published in *Science* on 10 November 1961, which was later included in a volume, *Cause and Effect*, edited by Daniel Lerner, published by the Free Press (New York) and Collier-MacMillan Limited (London) in 1965.

[2] Since the 1970s, Mayr's proximate-ultimate distinction has often been merged with Niko Tinbergen's famous four problem of ethology (1963), namely, the problem of causation, the problem of survival value, the problem of evolution, and the problem of ontogeny, which became an influential framework for research on animal behaviour. According to a popular view (e.g. Sherman 1988; Nesse 2019), Tinbergen's four problems are regarded as a finer-grained account of Mayr's proximate–ultimate distinction in the way that survival value and evolution are grouped together as ultimate while causation and ontogeny are grouped as proximate. However, as Brandon Conley (2020) argues, it is mistaken to construe Tinbergen's four problems as a simple refinement of Mayr's distinction. For this reason, I will not discuss Tinbergen's four problems in detail in this paper.

One may easily have a puzzling impression even when taking a quick look at the literature of the controversy: many contenders seem to talk past each other. The proximate-ultimate distinction is interpreted differently. Thus, it seems necessary to revisit and disambiguate the usage of 'the proximate-ultimate distinction' in the literature in order to make a careful examination of the controversy. This paper takes an integrated history and philosophy of science approach (aka an integrated HPS approach) to examining the debate over the proximate-ultimate distinction. Like other integrated HPSers (e.g. Arabatzis and Schickore 2012; Arabatzis and Howard 2015), I contend that integrated HPS should be both a good philosophy of science and a good history of science at the same time.[3] Thus, in this paper, I offer not only a philosophical examination of the debate over the proximate-ultimate distinction itself, but also an analysis of the historical development of the distinction. Firstly, I revisit Mayr's view on the proximate-ultimate distinction and its historical context (section 2). Secondly, I offer a critical analysis of the recent debate over Mayr's proximate-ultimate distinction (section 3). Thirdly, I examine the distinction in the context of the debate over the Modern Synthesis and Extended Evolutionary Synthesis (section 4). Finally, I argue for a functional approach to the debate (section 5).

2. Putting Mayr's Proximate-Ultimate Distinction Back into History

2.1 Mayr on the Proximate-Ultimate Distinction

In Mayr's MIT lecture, the proximate-ultimate distinction was introduced on the basis of his reflection on biology as an academic discipline. To a great extent, his proximate-ultimate distinction is derived from another distinction: the distinction between functional biology and evolutionary biology.[4] For Mayr, biology in the early 1960s can be divided into two branches.

> The word biology suggests a uniform and unified science. Yet recent developments have made it increasingly clear that biology is a most complex area-indeed, that the word biology is a label for two largely separate fields which differ greatly in methods, *Fragestellung*, and basic concepts. As soon as one goes beyond the level of purely descriptive structural biology, one finds two very different areas, which may be designated functional biology and evolutionary biology. (Mayr 1961, 1501)

Mayr argued that functional biology and evolutionary biology differ in three main respects. First of all, they differ in their research problems. Functional biology focusses on answering 'how' questions: how do certain structural elements (e.g. organs) operate, interact, and function? More precisely speaking, functional biologists deal with 'all aspects of the decoding of the programmed information contained in the DNA code of the fertilized zygote' (Mayr 1961, 1502). Evolutionary biology is mainly concerned with 'why' questions: why is there a particular characteristic of some organisms? In other words, evolutionary biologists are 'interested in the history of [the DNA] codes of information and in the laws that control the changes of these codes from generation to generation' (Mayr 1961, 1502).

Second, functional biology and evolutionary biology differ in their research methods. The main method of functional biology is experiment. For Mayr (1961, 1502), functional biologists' approach is 'essentially the same as that of the physicist and the chemist'.

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[3] For an elaboration of integrated history and philosophy of science, see Arabatzis and Howard (2015, 1–2) and Shan (2020a, 5–6).

[4] Functional biology includes molecular biology, cell biology, and biochemistry (Morange 2011).

Evolutionary biologists, however, pay much attention to the 'historical background' of the existing characteristics of organisms by studying 'the steps by which have evolved the miraculous adaptations so characteristic of every aspect of the organic world' (Mayr 1961, 1502).

Third, functional biology and evolutionary biology are distinct about their basic concepts, especially the concept of 'cause'. Mayr used an example of bird migration to illustrate the difference. When one asks what the cause of bird migration is, Mayr argued that there are four senses of the cause in this context: ecological cause, genetic cause, intrinsic physiological cause, and extrinsic physiological cause. Ecological causes of bird migration refer to some ecological factors (e.g. lack of food). A genetic cause is what is induced by the genetic constitution of bird. Intrinsic physiological causes refer to some physiological factors in response to some environmental changes, while extrinsic physiological causes are some external factors (e.g. temperature drop) that influence the behaviour of bird. For Mayr, functional biologists are interested in intrinsic and extrinsic physiological causes, while evolutionary biologists are concerned with ecological and genetic causes. Mayr further proposed that intrinsic and extrinsic physiological causes can be understood as 'proximate causes' and ecological and genetic causes are 'ultimate causes'. More formally, Mayr (1961, 1503) defined proximate causes as what 'govern the responses of the individual (and his organs) to immediate factors of the environment', while ultimate causes are what are 'responsible for the evolution of the particular DNA code of information with which every individual of every species is endowed'.

Mayr's distinction between proximate and ultimate causes suggests a version of conceptual (causal) pluralism: there are two concepts of cause in biology. These two concepts of cause are rooted in two branches of biology and correspond to two approaches to causal enquiry in biology respectively. This is a view that Mayr had consistently maintained for decades. Mayr (1993, 94) contended that a distinction between proximate and ultimate causes is 'useful' and 'widely adopted'.

2.2 The Proximate-Ultimate Distinction in the History of Ethology

It is worth highlighting that the terms 'proximate cause' and 'ultimate cause' were not Mayr's coinage. Neither was Mayr the first to distinguish ultimate causes from proximate causes in the context of biology. As Mayr (1993, 94) himself later pointed out, 'partitioning of causes goes back in biology at least one hundred years'. As early as at the beginning of the twentieth century, E. A. Schäfer (1907, 161) explicitly analysed bird migration in terms of 'ultimate cause' and 'immediate determining cause'. And in the first half of the twentieth century, these notions were widely employed in the fields like ethology (see, for example, Thomson 1926; Baker 1938). In particular, A. Landsborough Thomson explicitly highlighted the significance of a distinction between causal concepts in the analysis of bird migration.

> [T]he question of actual causation seems to have a *dual* aspect. The *ultimate cause* of migration must surely lie in the existence of the inborn habit and in the nature of the forces in the far past which gave it origin. In the second place there must be *immediate stimuli*, periodically recurring, which evoke the habit to active expression each autumn and each spring. (Thomson 1924, 639; my emphasis)

He further expounded 'ultimate cause' and 'immediate stimuli' in terms of four factors.

> (a) Factors which… may make migration advantageous and thus give the custom a survival value; (b) Factors which may in the past have helped to originate and develop the custom in the race; (c) Factors which periodically stimulate the custom to active expression in the individual at the proper season ...; and (d) Factors which determine the manner in which migration is actually performed. (Thomson 1926, 264)

That said, Thomson maintained that the explanations by appealing to the different concepts of cause are not necessarily conflicting or competing. Rather they are complementary.

> [L]et us make sure that the distinction between the two kinds of causative factor is clearly understood. One is the remote original cause; the other is the recurring immediate cause. *Both are necessary to explain the existence and operation of instinctive behaviour*. There are, on the one hand, the factors which have implanted the capacity in the race, and which have shaped its subsequent evolution. There are, on the other hand, the factors which evoke the active expression of the behaviour at the appropriate times, twice in each year. The contrast is between the hand that packs the explosive charge in the cartridge, and the finger that pulls the trigger to release the latent force. (Thomson 1942, 153–54 my emphasis)

It is clear that, as John Beatty (1994, 342–43) indicates, Mayr's four senses of cause basically followed Thomson's four categories of the causes of migration. More precisely speaking, Mayr's ecological causes, genetic causes, intrinsic physiological causes, and extrinsic physiological causes are the refined version of Thomson's factors (a), (b), (c), and (d) respectively.[5] Furthermore, Mayr shared Thomson's view on the complementarity of ultimate and proximate causes. Following Thomson, Mayr insisted that neither a study of proximate causes nor a study of ultimate causes alone can offer a complete causal explanation of a given biological phenomenon.

> There is *always* a proximate set of causes and an ultimate set of causes; *both* have to be explained and interpreted for a *complete* understanding of the given phenomenon. (Mayr 1961, 1503; my emphasis)

2.3 The Proximate-Ultimate Distinction and the Molecular Revolution

It is also worth noting that Mayr's defence of the proximate-ultimate distinction played an important role in his defence of the significance of evolutionary biology and the autonomy of biology as an academic discipline. In the 1950s, especially after James Watson and Francis Crick's work on the structure of DNA, a new branch of biology, molecular biology or 'functional biology' called by Mayr (1961), quickly developed and gained in prestige. In contrast, evolutionary biology was struggling to compete with molecular biology for status and funding (Smocovitis 1992; Beatty 1994; Dietrich 1998). As George Simpson complained, there was a 'band wagon effect' of molecular biology at the time.

> The rate of progress [in biology] is uneven, and rapid advances take place now in one direction and now in quite another. Once a shove has been given in one direction, perhaps by a technological or conceptual breakthrough, perhaps by individual enthusiasm, perhaps by what seems pure chance, a band wagon

[5] Mayr's adoption of Thomson's concepts began in a paper, "Theoretisches Zur Geschichte Des Vogelzuges", co-authored with Wilhelm Meise in 1930.

> ensues. Students flock to the accelerating front; money is poured into it; professional advancement, fame, and fortune follow it… The gaudiest band wagon just now is manned by reductionists, travels on biomedical and biophysical roads, and carries a banner with a strange device: DNA. (Simpson 1964, 113–14)

Mayr was also deeply concerned with the unbalanced disparities in status and funding between classical and new sciences, in which evolutionary biology was then labelled as a 'classical', 'old fashioned' or 'passé' science.

> The most imaginative workers are those who have been attracted to the new efforts and have thus automatically left the more orthodox workers in command of the classical fields [e.g. evolutionary biology]. Bright young students quite naturally look for the greenest pastures. Recruitment thus becomes a serious problem. This is aggravated by the attitude of the Young Turks in the new areas [e.g. molecular biology]. They tend to regard the more classical branches of their science with unconcealed contempt. At worst, this intolerance leads them to attempt to cut off funds from the more, classical fields. The situation is further aggravated by the attitude of some foundations and science administrators. They are justified in fostering exploitation of breakthroughs, but it seems unwise for them to pour most of their funds into the glamor fields. (Mayr 1963, 763)

It was the time when, as E. O. Wilson (1994, 228) later recalled, evolutionary biologists 'were forced by the threat to rethink [their] intellectual legitimacy'. What is worse, the rise of molecular biology in the 1950s and 1960s fuelled a reductionist account of biology and led to a 'crisis' in biology (Simpson 1967). There are two senses of the reducibility of biology. The first is the view that all other branches of biology would be eventually reducible to molecular biology. As Simpson (1967, 363) indicated, there was 'a missionary fervor for molecular biology as real biology, the biology of the future'. George Wald, a well-known biochemist and Nobel laureate, is said to declare that molecular biology is just 'the whole of biology' (Mayr 2004, 70).

The second is the view that biology is ultimately reducible to the physical sciences: answers to biological questions 'can often be put in terms of the physical sciences' (Simpson 1964, 104). As V. Betty Smocovitis (1992, 58) points out, 'As research in molecular biology and biochemistry intensified, the links between physicists and chemists and biologists solidified further. With the articulation and refinement of the molecular basis for genetic change, biology faced its greatest threat of complete engulfment by the physical sciences'.

It is evident that the first sense of the reducibility of biology undermines the significance of evolutionary biology while the second challenges biology as an autonomous academic discipline. Such a reductionist picture of biology was strongly resisted by some leading evolutionary biologists at the time. For example, Theodosius Dobzhansky argued for the equal status of evolutionary biology and molecular biology.

> At present both molecular and organismic biology seem ready for major new advances. The prime consideration here should perhaps be that they should advance not separately, not in isolation, but together, in cooperation. A British politician opined that in politics scientists "should be on tap, not on top"; in biology, molecular and organismic biologists should be on tap for each other, and neither should be on top of the other. (Dobzhansky 1966, 550)

Simpson was also highly critical of the reductionist account of biology by arguing that evolutionary biology and molecular biology differ in their levels of research: evolutionary biologists focus on the organismal and population levels, whereas molecular biologists are concerned with the molecular level.

> From here on the molecular biologists have a lot of interesting but plodding work to do in accumulating more knowledge at their level, just as the evolutionary biologists, although they are further along, still have at their level. (Simpson 1967, 375)

Moreover, Simpson (1967) argued that there are three fundamental differences between the physical and biological sciences: biological systems are more complex than physical systems; the biological sciences are largely about individual phenomena while the physical sciences are more about general patterns of individual phenomena; the biological sciences have historical elements while the physical sciences do not.

Like Dobzhansky and Simpson, Mayr defended the significance of evolutionary biology as an important branch of biology.

> We live in an age that places great value on molecular biology. *Let me emphasize the equal importance of evolutionary biology*… Fortunately the large number of biologists who continue to cultivate the evolutionary vineyard is an indication of how many biologists realize this: we must acquire an understanding of the operation of the various factors of evolution not only for the sake of understanding of our universe, but indeed very directly for the sake of the future of man. (Mayr 1976, 326; my emphasis)

As a long-term critic of the reductionist account of biology, Mayr was persistently opposed to any attempts to reduce biology to the physical sciences.

> [A]dvances in our understanding of the microworld of subatomic particles are not going to make any explanatory contributions to our understanding of the middle world [e.g. biological phenomena]. (Mayr 1988, 475)

> [N]o principle of historical evolutionary theory can ever be reduced to the laws of physics or chemistry. (Mayr 2004, 79)

His defence of the proximate-ultimate distinction was key to his defence of the anti-reductionist account of biology. To a great extent, Mayr's lecture 'Cause and Effect in Biology' was structured and framed in a way to respond to an earlier lecture in the Hayden Colloquium, 'Types of Causal Explanation in Science', delivered by Ernest Nagel, a philosopher of science famous for his account of intertheoretic reduction (e.g. Nagel 1961). Mayr began his lecture by identifying three elements of causality (i.e. explanation, prediction, and teleology), which he attributed to Nagel.[6]

[6] It should be emphasised that Mayr misrepresented Nagel's view here. In his lecture, Nagel did not regard explanation, prediction, and teleology as three constitutive elements of causality. Nor did Nagel define causality in terms of explanation, prediction, and teleology. Rather Nagel merely claimed that the concept of causality is often used in the contexts of explanation, prediction, and teleology (Nagel 1965, 12–13). And the aim of Nagel's lecture was to examine 'the use of causal notions that arise in these three contexts of analysis' (Nagel 1965, 13).

> Causality, no matter how it is defined in terms of logic, is believed to contain three elements: (i) an explanation of past events ("a posteriori causality"); (ii) prediction of future events; and (iii) interpretation of teleological – that is, "goal-directed" – phenomena. (Mayr 1961, 1501)

He examined these three elements of causality in the context of biology and concluded that they are not essential to the concept of causality in biology. In short, Mayr's lecture aimed at a critique of the application of the concept of causality in the physical sciences to the biological sciences.[7] He ended his lecture with four main conclusions.

1) Causality in biology is a far cry from causality in classical mechanics.
2) Explanations of all but the simplest biological phenomena usually consists of sets of causes. This is particularly true for those biological phenomena that can be understood only if their evolutionary is also considered. Each set is like a pair of brackets which contains much that is unanalyzed and much that can presumably never be analyzed completely.
3) In view of the high number of multiple pathways possible for most biological processes (except for the purely physicochemical ones) and in view of the randomness of many of the biological processes, particularly on the molecular level (as well as for other reasons), causality in biological systems is not predictive, or at best is only statistically predictive.
4) The existence of complex codes of information in the DNA of the germ plasm permits teleonomic purposiveness. On the other hand, evolutionary research has found no evidence whatsoever for a "goal-seeking" of evolutionary lines, as postulated in that kind of teleology which sees "plan and design" in nature. The harmony of the living universe, so far as it exists, is an a posteriori product of natural selection. (Mayr 1961, 1506)

In a nutshell, Mayr highlighted the significance of evolutionary biology and argued for the autonomous character of biology. From a historical point of view, Mayr's defence of the proximate-ultimate distinction arose when he, with other leading evolutionary biologists (e.g. Dobzhansky and Simpson), found it necessary and urgent to respond to the threat from the success of molecular biology and ward off 'reduction to the physical sciences' (Smocovitis 1992, 59). In order to 'secure the place of evolutionary biology in the biology of the future', as Beatty (1994, 349) indicates, '[Mayr] used the proximate/ultimate distinction over and over again in correspondence and in conferences to make the point that there is more to biology than the study of proximate causes'. The proximate-ultimate distinction, for Mayr, helps to defend the significance of evolutionary biology. It also helps to defend the 'special character and autonomy of biology' (Beatty 1994, 339). In other words, Mayr's defence of the proximate-ultimate distinction was rooted in his defence of evolutionary biology and biology in general.

3. Reconstructing and Reexamining the Debate over the Proximate-Ultimate Distinction

3.1 Two Foci of the Debate

The debate over Mayr's proximate-ultimate distinction has been centred on two issues: the semantic issue and the stance issue. The semantic issue focusses on the very meaning of Mayr's concepts, including proximate cause, ultimate cause, 'how' question, and 'why'

[7] However, as I mentioned in footnote 6, Mayr's target was in fact a caricature of Nagel's definition of causality.

question. The stance issue is about the philosophical theses underlying Mayr's proximate-ultimate distinction. Although Mayr's proximate-ultimate distinction is often construed as the distinction between proximate and ultimate causes, I would like to emphasise that it has a richer content. As I have shown in section 2, Mayr's distinction between proximate and ultimate causes is entangled in his methodological reflection on biology: there are two branches of biology, which differ in their research problems, methods, and concepts. Accordingly, Mayr's proximate-ultimate distinction reflects his four stances.

- **Stance on causal questions.** There are two types of causal questions in biology: 'how' questions and 'why' questions. (Exploratory pluralism)
- **Stance on causal methodologies.** There are two approaches to causal enquiry in biology: functional approach and evolutionary approach. (Methodological pluralism)
- **Stance on causal explanations.** There are two types of causal explanation in biology: proximate explanation and ultimate explanation. (Explanatory pluralism)
- **Stance on causal concepts**. There are two concepts of cause in biology: proximate cause and ultimate cause. (Conceptual pluralism)

All of these stances have their roots in Mayr's lecture in 1961. As I have mentioned, Mayr is explicit on the point that functional biology and evolutionary biology differ in their research problems, methods, and concepts in causal enquiry. Proximate and ultimate causes are employed in two different types of explanation to answer two different types of questions (i.e. 'how' questions and 'why' questions). These differences between functional biology and evolutionary biology suggest two different approaches to causal enquiry in biology. It is evident that Mayr's four stances are related to each other, as shown in Figure 1. On the one hand, the distinction between causal questions and the distinction between causal methodologies imply the distinction between causal explanations, which leads to the distinction between causal concepts. On the other hand, the distinction between causal concepts and the distinction between causal explanations reflect the distinction between causal questions and the distinction between causal methodologies.

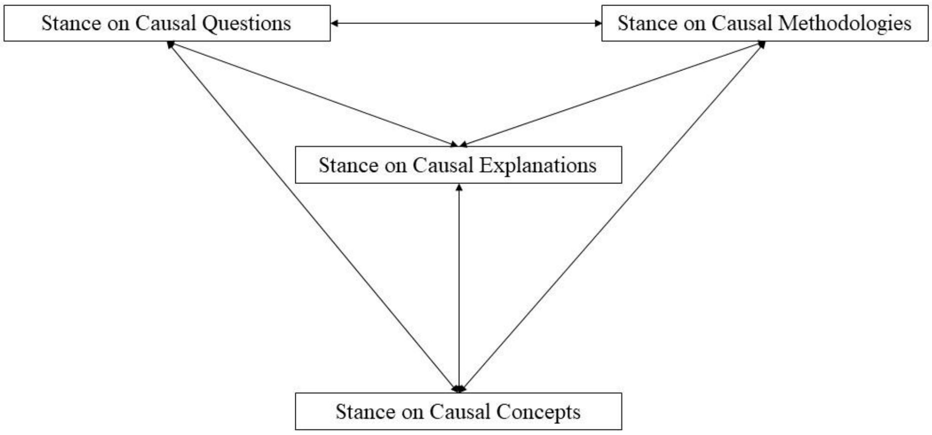

Figure 1. Mayr's Four Stances

3.2 The Semantic Issue

Earlier objections to Mayr's proximate-ultimate distinction are more concerned with the semantic issue. For example, Richard Francis (1990) is very nervous about the ambiguous meaning of 'ultimate'.[8]

> [I]f there are, say, a series of ten characterizable influences on an event which can be ordered serially in time, we can call influence number "10" the most proximate, and influence number "1" the least proximate. But does that make influence number "1" the ultimate cause? (Francis 1990, 401)

André Ariew (2003) provides a more sophisticated semantic objection to Mayr's distinction. He argues that Mayr's concept of proximate cause, defined in terms of some dated notions such as 'decoding the genetic program', fails to capture the development of biology in the second half of the 20th century.

> Mayr's discussion of genetic information is completely inappropriate to the issue of what makes developmental biology a study of "proximate causes". Developmental biology [is] much more than the study of the DNA molecule. (Ariew 2003, 556)[9]

He is also critical of Mayr's concept of ultimate cause, which appeals to natural selection alone.

> Mayr takes evolutionary biology to be the exclusive study of adaptations *qua* products of natural selection. He writes, "[ultimate causes] are causes that have a history and that have been incorporated into the system through many thousands of generations of *natural selection*" (p. 1503, my italics). However, natural selection is only one explanation of nature's "diversity". Indeed, natural

[8] Donald Dewsbury (1999) has a similar concern about the meaning of 'ultimate'.
[9] For a similar objection, see Birch (2017).

> selection is one explanation of how populations evolve. There are others: migration, mutation, genetic recombination, and drift. If all of these other sorts of explanations answer the appropriate evolutionary questions, then they too should be included as part of the conception that undergirds "ultimate" explanations. (Ariew 2003, 558)

David Haig (2013) finds the meaning of 'why' in 'why' questions in the debate over Mayr's proximate-ultimate distinction ambiguous. They can refer to 'what for' questions or 'how come' questions. Haig notes that while Mayr explicitly refers 'why' questions to 'how come' questions, many contenders in the debate still construe 'why' questions as 'what for' questions. These inconsistent uses of 'why' questions led to the ambiguity in the meaning of ultimate causes. Thus, Haig suggests that the term 'ultimate causes' should be abandoned.

3.3 The Stance Issue

The contenders in the recent debate over Mayr's proximate-ultimate distinction are more interested in the stance issue. Kevin Laland and his associates (Laland et al. 2011; 2013) famously challenge Mayr's stance on causal concepts. Although they admit that Mayr's distinction between proximate and ultimate causes can be helpful to study some simple biological phenomena such as bird migration, Laland et al. argue that many complex biological phenomena cannot be well accounted for by identifying proximate causes and ultimate causes separately. Consider a case of intersexual selection. The peacock's tail evolves through mating preferences in peahens, and those preferences co-evolve with the male trait. If one tries to apply Mayr's concepts of proximate cause and ultimate cause, it can be argued that the ultimate cause of the male trait is the prior existence of the female's mating preference. However, the female's mating preference, manifest in peahen mate-choice decisions, is shaped by inherited tendencies and modified by experience throughout development, which co-evolves with the mate trait. For Laland and his associates, this is contrasted with the case of bird migration. The migrating behaviour of birds evolves through a unidirectional process in the sense that the migrating behaviour is basically shaped by selection only to respond to certain features in the external environment. This suggests that developmental processes do not matter much in ultimate causes. In the case of intersexual selection, the evolution of the peacock's tail is a reciprocal process in two senses: the ultimate cause of the male trait is the female's mating preference which is itself a product of evolution and development; developmental processes play a role in both ultimate and proximate causes. In other words, the evolution of the peacock's tail is not influenced by the peahen's mate-choice unidirectionally: it is not a mere response to the peahen's mate-choice. It also contributes to shape the peahen's mate-choice dynamically. Accordingly, developmental processes do feature in the ultimate cause. Thus, the ultimate cause and the proximate cause of the male trait are mutually intertwined and overlap. In other words, the distinction between proximate and ultimate causes seems to be blurred. As a result, Laland and his associates (Laland et al. 2011; 2013) argue for a concept of reciprocal causation in biology: a causal explanation in biology 'must include an account of the sources of selection (as these are modified by the evolutionary process) as well as the causes of the phenotypes subject to selection'.[10] They argue that the concept of reciprocal causation captures a variety of causal

[10] It should be emphasised that Laland and his associates use the term 'reciprocal causation' in two different senses. First, reciprocal causation assumes a reciprocal account of causal relationships. Second, reciprocal causation refers to a type of evolutionary process where developmental processes 'share with natural selection some responsibility for the direction and rate of evolution and contribute to organism-environment complementarity' (Laland et al. 2015b, 2). It is clear that the second sense of reciprocal

phenomena in the biological sciences. Even cases of unidirectional selection (e.g. bird migration) can be construed as special cases of reciprocal causation.

Moreover, Laland and his associates question Mayr's stance on causal methodologies. They find Mayr's dichotomy between functional and evolutionary approaches problematic. They argue that the assumption behind such a distinction overlooks the interaction between developmental and evolutionary processes. In their words, the distinction between causal methodologies reflects 'an incorrect view of development that fails to address the origin of characters and ignores the fact that proximate mechanisms contribute to the dynamics of selection' (Laland et al. 2011, 1515).

Furthermore, Laland et al. argue that Mayr's stances on causal concepts and causal methodologies may impede progress in the biological sciences and suggest that it might be better abandoned: 'To the extent that researchers view the proximate/ultimate distinction as a barrier to the satisfactory integration of evolution and development' (Laland et al. 2011, 1516).[11]

It might seem to some that Laland et al.'s argument against Mayr's proximate-ultimate distinction applies a simple rule of logic, *Reductio ad absurdum*: the distinction between proximate and ultimate causes entails a unidirectional account of causation, which reflects an incorrect or incomplete view of development and evolution. Therefore, the distinction should be abandoned in practice. However, what is at issue is more than a logical issue. Even for those who agree with Laland et al. on their objections to Mayr's distinction, replacing the proximate-ultimate distinction with the concept of reciprocal causation is not the only option. As Jonathan Birch puts it,

> I agree with Laland et al. about the importance of these processes [e.g. niche construction, developmental plasticity, and social learning], and about the misleading nature of the 'genetic program' concept – and hence of the proximate-ultimate distinction as Mayr conceived it – when these processes are at work. But I see this as a reason to frame the proximate-ultimate distinction in a different way – a way more accommodating of the sorts of processes Laland et al. highlight – rather than a reason to abandon it altogether. (Birch 2017, 5)

Birch suggests that 'a useful proximate-ultimate distinction' can be drawn if proximate cause and ultimate cause are redefined as follows.

> We can then say that the ultimate causes of a behavioural phenotype are those which explain the origin and maintenance, over evolutionary time, of its transmissible basis in a population of organisms; whereas the proximate causes of a behavioural phenotype are those which explain, in the context of the life

causation is not a causal concept, while the first implicitly suggests a concept of causation in biology. In the following, I shall use 'reciprocal causation' in the first sense for the sake of consistency, whereas I shall use other terms such as reciprocal processes when talking of the second sense.

[11] That said, Laland and his associates are sympathetic to Mayr's stances on causal questions and on causal explanations to some extent: proximate and ultimate explanations are complementary to each other and it is legitimate and helpful to ask 'how' questions and 'why' questions.

> Mayr's concern that proximate and ultimate explanations should not be regarded as alternatives remains entirely valid today and is an important and useful heuristic that applies broadly across biological disciplines. There will always be how and why questions, and their answers will always be complementary rather than conflicting. (Laland et al. 2011, 1515)

> cycle of a particular organism, the relationship between the phenotype's transmissible basis and its manifest form. (Birch 2017, 5)

It should also be highlighted that Laland and this associates do not dismiss the distinction between proximate and ultimate causes completely. They do not try to argue that there are no such a distinction between proximate and ultimate causes. Rather what they really reject is the view that proximate causes and ultimate causes are exclusive to each other.

Contra Laland and his associates, Thomas Dickins and R. A. Barton (2013) defend Mayr's stance on causal concepts. They accuse Laland et al. of misunderstanding Mayr's concept of ultimate cause. Dickins and Barton maintain that Mayr (1961, 1503) construes ultimate causes as having a history while Laland et al. (Laland et al. 2011, 1512) conflate ultimate causes with historical explanations. They argue that Laland et al.'s 'assiduous' reading of Mayr might prevent some scientists from exploring the dynamics of change in intersexual selection, while Mayr's original account of ultimate causes does not (Dickins and Barton 2013, 754–55). They further argue that intersexual selection as well as other complex biological phenomena can be well characterised in terms of proximate causes and ultimate causes: 'the proximate-ultimate distinction allows us to make sense of biological causation as Mayr described, and that … this included the complex and dynamic phenomena that Laland et al. report in their papers' (Dickins and Barton 2013, 754). Moreover, Dickins and Barton challenge the concept of reciprocal causation as a genuine alternative to the concepts of proximate cause and ultimate cause. They insist that the concepts of proximate cause and ultimate cause are somehow indispensable to explain the reciprocal processes: 'in order to understand the complex story of peacock and peahen phenotypes Laland et al. have to invoke proximate and ultimate causes, as defined by Mayr' (Dickins and Barton 2013, 750). Not only do they defend Mayr's stance on causal concepts, Dickins and Barton but also try to allay the concerns about his stances on causal questions, causal methodologies, and causal explanations.

> We very much doubt that Laland et al would deny the utility of asking how a trait operates and why the trait exists. (Dickins and Barton 2013, 754)

> It seems that [Laland et al.'s] core concern is that of scientific interests and they fear that an assiduous reading of Mayr (1961) might prevent some scientists from exploring the dynamics of change in intersexual selection and elsewhere… But Laland et al. should not be so concerned on this score, as the kind of interaction across time that they pointed to for peacocks and peahens is standard fare in the introductory textbooks, and not only during discussion of intersexual selection. (Dickins and Barton 2013, 754–55)

> Any explanatory work associated with the use of [reciprocal causation] has to rely on a clear understanding of proximate and ultimate causation. (Dickins and Barton 2013, 756)

To some extent, Dickins and Barton provides a full-fledged defence of Mayr's stances on causal questions, causal methodologies, causal explanations, and causal concepts. Although they might not fully accept Mayr's original definitions of proximate cause and ultimate cause, they maintain that 'proximate cause' and 'ultimate cause' are important conceptual tools to study various phenomena of animal behaviour.

Francis, though most of his objections focus on the semantic issue, has a stance objection. He is explicitly sceptical of the legitimacy of 'why' questions in biology and uncomfortable with the underlying teleological attitudes (Francis 1990, 407–8). Brett Calcott (2013) also criticises Mayr's stance on causal questions. He provides a fine-grained analysis of causal questions by distinguishing temporal causal questions from explanatory causal questions. For Calcott, there are two types of temporal causal questions: synchronic questions and diachronic questions. Synchronic questions are about how things change over time, while diachronic questions about how things work at a time. There are also two types of explanatory causal questions: individual-based questions and population-based questions. Individual-based questions are about individual mechanisms, whereas population-based questions about processes of change in populations. Calcott (2013, 772) suggests that Mayr's 'how' questions and 'why' questions can be roughly understood as synchronic/individual questions and diachronic/population questions as follows respectively.

> How question: how do individuals work at a time?

> Why question: how do populations change over time?

However, he argues that the following important type of questions cannot be captured in terms of these questions.

> Diachronic/individual question: how do individuals change over time?

In short, Calcott complains that Mayr's distinction between 'how' questions and 'why' questions overlooks the complexity of research problems in biology and 'fails to capture the full range of questions we can ask' (Calcott 2013, 769).

Despite his objections to Mayr's concepts of proximate cause and ultimate cause, Ariew (2003) is sympathetic to Mayr's stance on causal explanations: there are two types of causal explanation in biology. That said, he characterises them quite differently. First, Ariew talks of evolutionary explanation instead of ultimate explanation. As discussed earlier, he is unsatisfied with Mayr's definition of ultimate cause, but he agrees with Mayr on the point that evolutionary biologists seek to explain 'why' questions (e.g. why certain traits have become prevalent in populations). And he suggests that the term 'evolutionary explanation' better captures this type of explanation. Second, Ariew's distinction between proximate explanation and evolutionary explanation is different from Mayr's. For Ariew, proximate explanations are individual-level causal explanations that answer questions about an organism over its lifetime, while evolutionary explanations are statistical explanations of population-level phenomena. He further argues that evolutionary explanations are distinct from and cannot be reduced to proximate explanations. In particular, Ariew argues that the latter are dynamical while the former not. A proximate explanation is dynamical in the sense that it must 'cite causal properties during an individual's lifetime including development and physiological processes' (Ariew 2003, 564). In contrast, evolutionary explanations are about 'statistical attributes of a population, not dynamical properties of individuals' (Ariew 2003, 560).

Moreover, Ariew argues explicitly for a distinction between 'how' questions and 'why' questions.

> [U]ltimate and proximate refer to two different explanations that answer *different sorts of questions*. Proximate explanations answer causal questions of individuals and the ultimate explanations answer questions about the prevalence and maintenance of traits in a population. (Ariew 2003, 559 my emphasis)

Accordingly, Ariew seems to embrace methodological pluralism as well.

> [T]here is an important distinction between the biological *study* of individual level causal events and the *study* of statistical level events pertaining to evolutionary change… [T]he individual level causal vs. statistical level evolutionary distinction should replace Mayr's proximate/ultimate distinction. (Ariew 2003, 557 my emphasis)

Jack Vromen (2017) also argues for Mayr's stance on causal explanations. He identifies three senses of the proximate-ultimate distinction: 'a distinction between different kinds of causes', 'a distinction between different episodes in the total causal chain leading to the behaviour', and 'a distinction between different sorts of explanatory projects' (Vromen 2017, 17–18).[12] Vromen maintains that the third sense can be retained whilst the first two senses should be rejected. He is not convinced by that the concept of reciprocal causation, developed by Laland et al. (Laland et al. 2011; 2013), provides a better alternative account of causation in biology than Mayr's distinction between proximate and ultimate causes. In particular, following Dickins and Barton, Vromen (2017, 15) insists that Laland et al.'s reciprocal analysis of complex biological phenomena such as intersexual selection 'presupposes rather than obviates the proximate—ultimate distinction'.

Raphael Scholl and Massimo Pigliucci (2015) defend a 'lean' version of the distinction between proximate and ultimate causes, in which the concepts of proximate cause and ultimate cause suggest different aspects of causation in biology. They are used to answer different types of contrastive causal questions.

> The proximate question asks *why* this bird flies south *in contrast to* another, otherwise identical bird that lacks the same neural mechanism. In contrast, the ultimate question asks *why* these birds fly south *in contrast to* another population of birds with a different history of natural selection. (Scholl and Pigliucci 2015, 661 my emphasis)

For Scholl and Pigliucci, neither a causal explanation in terms of proximate causes nor a causal explanation in terms of ultimate causes provides a complete causal account of a given evolutionary phenomenon. Rather they only highlight different aspects of a complete causal account. And these aspects may overlap. Such a reading of the distinction between proximate causes and ultimate causes does not imply that developmental processes are irrelevant to ultimate explanations. It is just that developmental processes carry little explanatory force in some evolutionary phenomena, such as bird migration. It is in this sense that Scholl and Pigliucci defend a lean version of the distinction between proximate explanation and ultimate explanation, which suggests different explanatory foci rather than different types of explanation. In short, Scholl and Pigliucci's charitable reading of Mayr's proximate-ultimate distinction highlights its pragmatic value in biological research: it is all about '[u]nder what circumstances [it is] appropriate for explanatory purposes to foreground or background

[12] Vromen's way of disambiguating the proximate-ultimate distinction is quite different from mine. For example, Vromen's first sense of the distinction seems to suggest a version of metaphysical causal pluralism: there are two kinds of causation in biology, namely, evolutionary processes and behaviour-generating mechanisms. I doubt that Mayr ever accepted that proximate and ultimate causations are two kinds of causation. I also doubt that any advocate of the proximate-ultimate distinction takes this particular metaphysical stance. As I have argued in section 2, Mayr's causal pluralism is more conceptual than metaphysical. Some might argue that Vromen's first sense of the distinction is a version of conceptual pluralism. If so, I cannot see why the first sense should be distinguished from the second sense, which is clearly a version of conceptual (causal) pluralism.

certain aspects of the complete causal account of any given evolutionary transition' (Scholl and Pigliucci 2015, 662).

Very recently, Grant Ramsey and Bendik Aaby (2022) argue for Mayr's stance on causal concepts by invoking the distinction between triggering causes and structuring causes. A structuring cause is typically defined as what sets up the structure of a causal system, while a triggering cause is what triggers the system to produce its effect (Ramsey 2016, 422). Ramsey and Aaby contend that the distinction between triggering causes and structuring causes sheds new light on Mayr's distinction between proximate causes and ultimate causes: 'one way of making sense of the causes underlying the [proximate-ultimate distinction] is to associate proximate with triggering causes and ultimate with structuring causes' (Ramsey and Aaby 2022, 17).[13] Consider a case of earthworms. It is well known that earthworms transform the soil that they are living in, making it more suitable for their own physiology by lowering the soil matric potential so that water is easier to obtain (and retain) from their physical surroundings. The altered soil is passed on to the subsequent generations through ecological inheritance. Therefore, there is a form of niche construction that involves trans-generational adaptive modification of the environment, which in turn produces selective effects. The effects of individual-level burrowing activities help to create a selective environment in which the population-level response is to retain a nephridia adapted to an aquatic, and not terrestrial, environment. In this case, the ultimate cause of the nephridia retention is the action of natural selection, which is part of a product of the structuring activities of the earthworms. In other words, the collective effect of individual-level burrowing activities is the ultimate cause of nephridia retention by playing a structuring causal role, whereas the proximate cause is the burrowing activities of individual earthworms. Ramsey and Aaby stress that a distinction between proximate causes and ultimate causes in terms of triggering and structuring causes does not imply that these causes are non-overlapping. What is more, they argue that Mayr's distinction between proximate causes and ultimate causes can be construed as an ontological distinction between two different kinds of causation.

3.4 Summary and Remarks

As discussed, there have been two foci of the debate over Mayr's proximate-ultimate distinction. One is about the semantic issue, the other the stance issue. If Mayr's proximate-ultimate distinction is taken literally, it is not very difficult to challenge his definitions of proximate cause and ultimate cause. It has been over 60 years since Mayr's lecture. With the development of the biological sciences, virtually few biologists and philosophers today still accepts Mayr's definitions of proximate cause, ultimate cause, 'how' question, and 'why' question without any modifications or refinements. An anachronistic, semantic objection to Mayr's concepts from a contemporary point of view is just too cheap.

Even though Mayr's definitions of proximate causes and ultimate causes are not defensible, the stances underlying Mayr's proximate-ultimate distinction are worthy of careful examination. In sum, there have been debates over conceptual pluralism, methodological pluralism, explanatory pluralism, and exploratory pluralism.[14] In general, conceptual pluralism and methodological pluralism are more controversial than explanatory pluralism

[13] The idea is not completely novel. It somehow echoes Thomson's analogy: the distinction between 'the remote original cause' and 'the recurring immediate cause' is analogous to the contrast between 'the hand that packs the explosive charge in the cartridge and the finger that pulls trigger to release the latent force' (Thomson 1942, 153–54).

[14] It seems clear that the debates over the stance issue go beyond what Mayr foresaw or could have foreseen.

and exploratory pluralism. Except that Calcott finds Mayr's 'why' questions in biology too simple and Francis is concerned with the teleological attitudes behind 'why' questions, most contenders appreciate the significance of the distinction between 'how' questions and 'why' questions in biological research. It is also widely accepted that there is a distinction between causal explanations. Nevertheless, it is under debate the nature of proximate explanations and ultimate (or evolutionary) explanations. For example, Ariew argues that proximate explanations and evolutionary explanations should be characterised as two different types of explanation, namely, individual-level causal explanations and population-level statistical explanations, while Scholl and Pigliucci maintain that the distinction between proximate and ultimate explanations merely suggest a contrast between different contrastive explanations rather than different types of explanation.

There is a more persistent and profound disagreement on conceptual pluralism and methodological pluralism, especially in the recent literature. Some (e.g. Laland et al. 2011; 2013) doubt the utility of the concepts of proximate cause and ultimate cause in contemporary biological sciences, while others (e.g. Dickins and Barton 2013; Scholl and Pigliucci 2015) still find them plausible. Laland and his associates' argument against the concepts of proximate cause and ultimate cause is highly influential among the sceptics of Mayr's proximate-ultimate distinction. However, it should be emphasised again that Laland and his associates' stance on causal concepts cannot be simply construed as a rejection of the distinction between proximate causes and ultimate causes. Rather they in fact challenge the exclusivity of proximate causes and ultimate causes, from a conceptual point of view. More precisely speaking, Laland and his associates might not prevent biologists from talking of proximate causes and ultimate causes instrumentally, but they maintain that these two concepts are intrinsically intertwined. Moreover, Laland and his associates are deeply concerned with the methodological implications of conceptual pluralism. They argue that Mayr's distinction between proximate cause and ultimate cause suggests a unidirectional account of causation, which has profound methodological implications.

> Mayr's unidirectional characterization of causation encourages focus on single cause-effect relations within systems rather than on broader trends, feedback cycles, or the tracing of causal influences throughout systems. It may also hinder the empirical investigation of evolutionary causes if the role of proximate processes goes unrecognized. This has consequences not only for biologists' ability to break new ground and integrate subfields within biology, but also influences biologists' view on how their discipline is connected to other sciences, including the humanities. (Laland et al. 2011, 1516)

Therefore, they contend that a distinction between causal methodologies based on a distinction between causal concepts will be unfruitful or even harmful. This is why Laland and his associates argue that the distinction between the concepts of proximate cause and ultimate cause is misleading and should be better replaced by the concept of reciprocal causation.

In contrast, Dickins and Barton insist that the distinction between proximate cause and ultimate cause does not assume or imply that proximate causes and ultimate causes are mutually exclusive to other. A distinction between proximate cause and ultimate cause still plays an important role in causal enquiry in the biological sciences.

4. Reconsidering the Proximate-Ultimate Distinction in the Context of the Debate over the Modern Synthesis and Extended Evolutionary Synthesis

As I have shown in section 2, Mayr's defence of the proximate-ultimate distinction was more than an attempt to develop a theory of causation in biology. It was part of his response to the reductionist account of biology given the rise of molecular biology in the 1950s and 1960s. The recent debate over Mayr's proximate-ultimate distinction also has significant methodological implications, especially for the ongoing debate over the Modern Synthesis (MS) and Extended Evolutionary Synthesis (EES).[15] The recent debate over Mayr's proximate-ultimate distinction, especially about Mayr's stance on causal concepts and causal methodologies, is intertwined with the debate over the MS and the EES. The concept of reciprocal causation is typically regarded as a core assumption of the EES.[16] As Laland et al. (2015a, 6) argue, the concept of reciprocal causation captures a central tenet of the EES: 'developing organisms are not solely products, but also causes, of evolution'. For Laland et al., a main problem of Mayr's proximate-ultimate distinction is that it is an indispensable component of the MS whose 'ability … satisfactorily to accommodate the rapid advances in developmental biology, genomics and ecology has been questioned' (Laland et al. 2015a, 1). Thus, it is no wonder that Laland et al. (Laland et al. 2011, 1512) argue that the proximate-ultimate distinction 'may now hamper progress in the biological sciences'. It is clear that Laland et al.'s challenge to Mayr's proximate-ultimate distinction was coupled with their advocate of the EES. In contrast, Dickins and Rahman's criticism on the EES is based on their defence of the distinction between proximate and ultimate causes: '[the EES's] focus on soft inheritance has led to a conflation of proximate and ultimate causation, which has in turn obscured key questions about biological organization and calibration across the life span to maximize average lifetime inclusive fitness' (Dickins and Rahman 2012, 2913). Dickins and Barton defend conceptual pluralism as well as the MS. They try to show that reciprocal processes can be well characterised by the proximate-ultimate distinction within the MS (Dickins and Barton 2013). However, Laland and his associates (Laland et al. 2013) are unconvinced by this proposal and insist that the distinction between proximate causes and ultimate causes should be better abandoned in practice.

It is very clear that much of the disagreement over conceptual pluralism and methodological pluralism is entangled with the disagreement over the MS and EES. That being said, not all the proponents of the EES accept a shift from the proximate-ultimate distinction to the concept of reciprocal causation.[17] For example, Scholl and Pigliucci still try to accommodate the proximate-ultimate distinction within the EES. They argue that their lean version of the proximate-ultimate distinction captures of the core assumption of the EES about reciprocal causation.

> A lean proximate–ultimate distinction—between biological mechanisms and evolutionary processes—should be maintained because proximate and ultimate causes answer different contrastive questions. It is entirely compatible with the view that developmental causes carry explanatory force in some evolutionary explanations. (Scholl and Pigliucci 2015, 668)

It is also clear that the stances on the proximate-ultimate distinction cannot be neatly mapped onto those on the MS-EES dichotomy. As shown in Table 1, while most proponents of the

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[15] For an overview of the debate over the MS and EES, see Shan (2024).
[16] It should be noted that, as I (Shan 2024) show, there are different versions of the EES. Proponents of the EES differ in their views on the nature and formulation of the EES.
[17] This is confirmed by Caleb Hazelwood's empirical study (Hazelwood 2023).

EES argue for the concept of reciprocal causation and most adherents of the MS maintain the significance of the proximate-ultimate distinction, there are some exceptions. These exceptional cases are revealing. One's stance on causal concepts is not necessarily a consequence of his stance on causal methodologies. As Hazelwood's survey (2023) shows, many biologists, who agree that the EES is a better framework than the MS, still resist the conceptual shift from the proximate-ultimate distinction to the concept of reciprocal causation. Therefore, we should not conflate the debate over the proximate-ultimate distinction with the debate over the MS and the EES.

Table 1. Views on the Proximate-Ultimate Distinction and the MS-EES Dichotomy		
	The MS	The EES
The proximate-ultimate distinction	Mayr (1961) Dickins & Barton (2013) Dickins (2021)	Scholl & Pigliucci (2015)
Reciprocal causation		Laland et al. (Laland et al. 2011; 2013) Sterelny (2013) Uller & Laland (2019)

Now let us go back to the arguments for reciprocal causation in the debate over the MS and the EES. Precisely speaking, Laland and his associates put forward two different arguments for the replacement of Mayr's proximate-ultimate distinction with reciprocal causation.

The argument for reciprocal causation by appealing to reciprocal processes

P1. Mayr's proximate-ultimate distinction assumes a unidirectional account of causation.

P2. A unidirectional account of causation fails to capture the reciprocal feature of many evolutionary processes.

P3. The concept of reciprocal causation captures the reciprocal feature of many evolutionary processes.

C. Mayr's distinction should better be abandoned and replaced by the concept of reciprocal causation.

The argument for reciprocal causation by appealing to the EES

P4. The concept of reciprocal causation is an indispensable component of the EES.

P5. Mayr's proximate-ultimate distinction is an indispensable component of the MS.

P6. The EES provides a more promising framework for evolutionary biology than the MS.

C. Mayr's distinction should better be abandoned and replaced by the concept of reciprocal causation.

I argue that neither of the arguments is decisive. The argument for reciprocal causation by appealing to reciprocal processes is invalid. First, that Mayr's proximate-ultimate distinction faces some problems does not imply that it is not amendable to be 'useful' in complex and dynamic cases such as intersexual selection. As I have shown, there have been some serious attempts to revise the concepts of proximate cause and ultimate cause. In a Kuhnian picture of scientific development, the existence of anomalies and crises is not sufficient to result in a scientific revolution. Likewise, the proximate-ultimate distinction cannot be simply rejected just because it is susceptible to some problems. As Hasok Chang (2011, 428) points out, each concept 'has a unique potential to change and develop in response to new facts and ideas'. Second, even if Mayr's proximate-ultimate distinction is shown to be susceptible to some serious problems and the concept of reciprocal causation is immune to these problems, it does not imply that the proximate-ultimate distinction ought to be replaced by reciprocal causation. It also has to be shown that reciprocal causation is not conceptually reducible to proximate cause and ultimate cause. In short, the conjunction of P1, P2, and P3 does not entail C.

The argument for reciprocal causation by appealing to the EES is also problematic: a strong argument for the replacement of the MS by the EES does not imply that the proximate-ultimate distinction should be replaced with the concept of reciprocal causation. A holistic change of scientific consensus does not prevent scientists from reasoning and talking in old terms. It is not unusual that after a scientific revolution some old concepts are still retained and employed. For example, physicists today still talk about mass, even if it means something different from what Isaac Newton thought of. What is more, it is still under debate whether there is a strong argument for the replacement of the MS by the EES.

In sum, I argue that these arguments for reciprocal causation are not strong enough to declare the death of the proximate-ultimate distinction.

5. Exploring Causal Concepts in Biological Practice

Although I am not convinced by Laland and his associates' call for the abandonment of the proximate-ultimate distinction, I appreciate their treatment of causal concepts in biology by examining them within its practical context. This instantiates the practice-based approach to scientific concept (e.g. Nersessian 2008; Feest 2010; Kindi 2012; Waters 2014; Shan 2020a), according to which, a scientific concept should be understood as a tool for scientists in practice rather than a mere linguistic entity. More specifically, as I (Shan 2020a, 146–47) argued, a scientific concept is a tool used in various intertwined activities in scientific practice, including problem-defining, problem-refining, problem-specification, hypothesisation, experimentation, and reasoning. Thus, we should understand conceptual practice in a broader context of scientific practice. Accordingly, we need to analyse and examine causal concepts within the context of scientific practice by scrutinising how a causal claim is established and what role a causal claim plays in various scientific activities. In addition, I also agree with Laland and his associates' emphasis on the heuristic role of causal concepts in scientific progress. Whether a scientific concept ought to be employed or abandoned depends on whether it contributes to scientific progress.

Therefore, I argue that a philosophical examination of the use of causal concepts in biology needs to be practice-based and articulate its role in scientific progress. To this end, I shall develop a criterion to determine whether a scientific concept ought to be employed in practice based on my function approach to scientific progress (Shan 2019; 2020a; 2022b), according to which, science progresses when more useful exemplary practices are proposed.[18] An exemplary practice is defined as a particular way of problem-defining and problem-solving, typically by means of problem-introduction, problem-refining, problem-specification, conceptualisation, hypothesisation, experimentation, and reasoning. An exemplary practice is useful when it provides a repeatable way of problem-defining and problem-solving which offers a reliable framework for further investigation to solve unsolved problems and generate novel problems across different areas. A good example of useful exemplary practices is Gregor Mendel's work on hybrid development (1866). By introducing novel research problems and their solutions (including novel concepts and ways of experimentation), Mendel provided a reliable framework, which was influential for the investigation of the problem of heredity in the early twentieth century.[19] Accordingly, I propose a functional criterion as follows.

> *A concept ought to be kept and employed in scientific practice if it contributes to a useful exemplary practice.*

Such a functional criterion well explains why some scientific concepts persisted for a long time while others abandoned. Consider the reception of the concept of dominance in the history of genetics. As I (Shan 2020a, chap. 8) show, the concept of dominance was widely received in the early 1900s because it played an important role in a continuous series of useful exemplary practices (e.g. de Vries 1900; Correns 1900; Bateson 1902) in the study of inheritance. In contrast, the significance of the concept of dominance faded away in the 1910s and 1920s because it was no longer an important component of T. H. Morgan's theory of the gene (1915; Morgan 1926) and was dispensable in the study of inheritance in the framework of classic genetics. In short, the rise and fall of the concept of dominance in the history of genetics is accounted for by the functional criterion.

Accordingly, whether a causal concept (e.g. proximate cause, ultimate cause, and reciprocal cause) ought to be employed in biological practice depends on whether it contributes to any useful exemplary practice. It is worth noting that the functional criterion particularly well accounts for why Mayr's proximate-ultimate distinction has been so influential and well received. As I have shown in section 2, the concepts of proximate cause and ultimate cause have been widely employed in ethological research since the first half of the twentieth century. And these causal concepts clearly contribute to various useful exemplary practices in the biological sciences. For example, the concepts of proximate cause and ultimate cause were widely used to study the diel vertical migration of zooplankton (e.g. Gabriel and Thomas 1987; Lampert 1989; Ringelberg 1993; 2010; Rinke and Petzoldt 2008). The proximate-ultimate distinction is assumed to offer a conceptual framework to study the physiological factors and evolutionary mechanisms of the phenomenon of diel vertical migration of pelagic animals in the freshwater and marine environments by distinguishing different research problems and approaches.

Now the key issue in the recent debate over Mayr's proximate-ultimate distinction is whether the concepts of proximate cause and ultimate cause can still be fruitfully employed in some

[18] For a systematic examination of the philosophical accounts of scientific progress, see Shan (2022a).
[19] For an in-depth analysis, see Shan (2020a, 86–96; 2020b, 394–402)

useful exemplary practices. Laland and his associates seem quite sceptical, while Dickins and his colleagues are rather optimistic. Laland and his associates contend that the EES provides a much more promising framework than the MS. Accordingly, they maintain that the replacement of Mayr's proximate-ultimate distinction with the concept of reciprocal causation is beneficial and constitutes a progressive shift from the MS to the EES. In contrast, Dickins and his colleagues insist that Mayr's 'proximate cause' and 'ultimate cause' are still important conceptual tools for biologists, especially ethologists, in practice.

I argue that it would be legitimate for Dickins and his colleagues to keep employing the concepts of proximate cause and ultimate cause to study animal behaviour as long as they can show how these causal concepts still contribute to useful exemplary practices. Likewise, it would also be rational for Laland and his associates to adopt the concept of reciprocal causation if they can successfully show how the concept of reciprocal causation is employed in some useful exemplary practices. However, it is unhelpful if scientists only pay lip service to their commitment to some causal concepts. Philosophical arguments alone do not justify the use of a causal concept in scientific research. Whether a scientific concept is used or abandoned is fundamentally a practical issue in the hands of scientists. A manifesto for the concept of reciprocal causation does not justify the replacement of the concepts of proximate cause and ultimate cause. The upshot is that the proof of reciprocal causation is in its use.

There is one clear advantage of taking the functional approach to causal concepts. Evolutionary biologists do not have to make an either-or choice between the proximate-ultimate distinction and reciprocal causation right now. By keeping using all of the concepts of proximate cause, ultimate cause, and reciprocal causation in different contexts, they are free to explore the use of different causal concepts in biological research. As I have highlighted, a causal concept typically comes bound up with some exemplary practices in which it plays a role. A plurality of the exploration of causal concepts will promote the development of causal methodologies and contributes to the development of biological research.

By further developing and revising the concepts of proximate cause and ultimate cause to accommodate novel findings from the fields like epigenetics, niche construction theory, and evo-devo, advocates of the proximate-ultimate distinction may be able to demonstrate the unique potential of the concepts of proximate cause and ultimate cause 'to change and develop in response to new facts and ideas'. On the other hand, by developing the corresponding methods to identify reciprocal causes and clarifying the role of reciprocal causation in answering 'why' questions and 'how' questions, proponents of reciprocal causation will be able to show the significance of reciprocal processes in evolutionary phenomena and show how evolution can be reconceptualised explicitly. Both might eventually inform the methodology of causal enquiry in the biological sciences and thus shed light on the debate over the MS and the EES ultimately. Therefore, taking the functional approach to causal concepts in evolutionary biology allows us to adopt a pluralistic stance on causal concepts. It will arguably promote a plurality of causal methodologies and lines of enquiry in the biological sciences.

Before concluding this section, I would like to ward off some potential misunderstandings of the functional approach and the pluralistic stance. First, taking the functional approach to causal concepts does not imply the acceptance of causal pluralism, whether in a metaphysical sense or a conceptual sense. Metaphysical causal pluralism maintains that there are different kinds of causal relationships *out there*, whereas conceptual causal pluralism is the view that there are distinct concepts of causation (e.g. Cartwright 2002; Hall 2004; Reiss 2009). It is clear that a pluralistic stance on causal concepts does not suggest that there are two kinds of causation in biology *out there*. Nor does it entail that there are two different concepts of causal relationships in biology. In the debate over the proximate-ultimate distinction, a pluralistic stance does not imply that reciprocal causation and proximate/ultimate causation are different ontological kinds of causation in evolutionary biology or fundamentally distinct concepts of causation in evolutionary biology. Although taking a functional approach may eventually inform our understanding of the metaphysical and conceptual nature of causation, it does not have immediate implications for the assessment of the philosophical debate over causal monism and causal pluralism.

Second, adopting a pluralistic stance does not necessarily impede the unification of biology. Consider the Mendelian-Biometrician controversy in the beginning of the twentieth century.[20] There were various approaches to the study of inheritance, including the Mendelian and Biometric approaches. The Mendelian approach was mainly developed by William Bateson (1902), based on Gregor Mendel's work (1866), while the Biometric approach was originally proposed by Francis Galton (1889) and mainly developed by Karl Pearson (1898) and W. F. R. Weldon (1905). In the early 1900s it was widely debated the main research problems, methods, and basic concepts in the study of heredity between the Mendelians and the Biometricians. In the heyday of the controversy, Pearson proposed a truce to the debate for three years, since he maintained that 'the controversy could only be settled by investigation, not by disputation' ("Zoology at the British Association" 1904, 539). Although Pearson's suggestion was not taken seriously at the time, it turns out that adopting a pluralistic stance behind Pearson's suggestion would have been beneficial. It played an important role in the Modern Synthesis, especially in the work of Fisher (1919; 1930), which contributed to a unified theory of evolution by integrating some of the Mendelian and Biometric methodologies and concepts. Adopting such a pluralistic stance in the 1900s might have advanced the development of the study of heredity to a greater extent. As Greg Radick (2023) suggests, adopting a pluralistic stance on the debate over Mendelism and Biometry (rather than a monistic stance by advocating Mendelism over Biometry) would have led us to what we now know about heredity much earlier. Thus, history tells us that adopting a pluralistic stance on scientific concepts often promotes rather than impedes the unification of biology.

Third, the pluralistic stance suggested by the functional approach to causal concepts should not be confused with Chang's pluralistic stance, namely active normative epistemic pluralism (2012). The key idea of Chang's pluralistic stance is that scientists ought to actively cultivate different lines of enquiry (or in Chang's term 'systems of practice'). I take active normative epistemic pluralism as an unconditional pluralistic stance because it suggests that different lines of enquiry ought be actively cultivated as many as possible. In contrast, the functional approach to scientific concepts suggests that only those concepts which contribute to useful exemplary practice ought to be employed. In other words, my pluralistic stance is to actively cultivate the causal concepts, each of which contributes to useful exemplary practices. For those causal concepts which do not contribute to useful exemplary practices, it is irrational to retain them in practice.[21] In other words, my pluralistic stance is not an unconditional pluralistic stance like Chang's.

[20] For a detailed analysis of the Mendelian-Biometrician controversy, see Provine (2001) and Shan (2021).

[21] Of course it is worth noting that there is another crucial difference between active normative epistemic pluralism and my pluralistic stance on scientific concepts. The former is a pluralistic stance on lines of

In sum, I argued that taking a functional approach to causal concepts and adopting a pluralistic stance on conceptual practice are beneficial for biological research, especially in the case of the debate over the proximate-ultimate distinction.

6. Conclusion

In this paper, I have taken an integrated HPS approach to the debate over the proximate-ultimate distinction in biology. From a historical point of view, I have revisited Mayr's distinction between proximate and ultimate causes and its context. In section 2, I have shown that Mayr's argument for the proximate-ultimate distinction was part of his defence of the significance of evolutionary biology and the autonomous character of biology. I have also shown that the concepts of proximate cause and ultimate cause have been widely employed in biology (especially ethology) since the early 20th century. From a philosophical point of view, I have scrutinised the arguments for and against the proximate-ultimate distinction. In section 3, I have distinguished two foci of the recent debate over the proximate-ultimate distinction: the semantic issue and the stance issue. I argued that the semantic objections to the distinction are often cheap, while the objections to the stances behind the distinction have more profound methodological implications. In section 4, I have examined the debate over the Modern Synthesis and the Extended Evolutionary Synthesis and its relation to the debate over the proximate-ultimate distinction. I argued that these two debates, though mutually intertwined, should not be conflated. A proponent of the proximate-ultimate distinction does not have to be a hardcore supporter of the Modern Synthesis, while an advocate of the Extended Evolutionary Synthesis does not necessarily embrace the call for the replacing the proximate-ultimate distinction with the concept of reciprocal causation. I also argued that none of the arguments in the debate over the proximate-ultimate distinction is decisive. Based on these historical and philosophical reflections, I have argued for a functional approach to causal concepts: the use of a causal concept depends on its contribution to useful exemplary practice. Accordingly, I argued that we ought to take a pluralistic stance on causal concepts in evolutionary biology.

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enquiry in scientific practice generally, while the latter on scientific concepts or conceptual practice specifically.

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