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Title. Incommensurability and the Extended Evolutionary Synthesis: Taking Kuhn Seriously

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Abstract. In this paper, we analyze the debate between the Modern Synthesis and the Extended Evolutionary Synthesis in light of the concept of incommensurability developed by Thomas Kuhn. In order to do so, first we briefly present both the Modern Synthesis and the Extended Evolutionary Synthesis. Then, we clarify the meaning and interpretations of incommensurability throughout Kuhn's works, concluding that the version of this concept deployed in *The Structure of Scientific Revolutions* is the best suited to the analysis of scientific disputes. After discussing incommensurability in Kuhn's works, we address the question of whether the Modern Synthesis and the Extended Evolutionary Synthesis can be considered semantically, methodologically, and ontologically incommensurable, concluding that they can. Finally, we discuss three problems that arise from such a conclusion: firstly, what

are the consequences of incommensurability; secondly, which mode of scientific change better explains this current dispute in evolutionary biology; and thirdly, whether rational theory comparison is possible given incommensurability. We suggest that the main consequence of incommensurability is profound disagreement, that the kind of scientific change that better explains the current dispute between the MS and the EES may be scientific specialization, and that incommensurability does not preclude rational theory comparison.
Keywords. Evolutionary Biology, Extended Evolutionary Synthesis, Modern Synthesis, Incommensurability, Thomas S. Kuhn, Scientific Specialization.

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1. Introduction

In recent years, a group of biologists and philosophers has claimed that the received view in evolutionary biology, known as the Modern Synthesis (henceforth MS), needs a rethink (*cf*. Laland et al. 2014). In particular, these authors claim that the MS has to be revised in order to take into account a series of recent discoveries made in various fields of the life sciences that could potentially affect at least some of its central tenets, including developmental plasticity (West-Eberhard 2003), niche construction (Odling-Smee et al. 2003), or inclusive inheritance (Jablonka and Lamb 2005; Jablonka 2017). To address these findings, these authors have proposed an allegedly "extended" version of the MS, which has been called the Extended Evolutionary Synthesis (henceforth EES) (Pigliucci 2007, 2009; Pigliucci and Müller 2010; Laland et al. 2015; Müller 2007, 2017). Calls for such an EES in evolutionary biology have been countered by several scientists who consider that the MS can fully account for these previous discoveries, giving rise to a sometimes heated debate between "reformist" proponents of the EES and the "conservative" defenders of the MS (e.g., Pievani 2015; Laland et al. 2014; Futuyma 2017; Müller 2017).

Debates about revising standard evolutionary theory are not new within evolutionary biology (e.g., Gould 1980; Stebbins and Ayala 1981). However, the current debate between the MS and the EES has gathered far more attention than previous discussions, in part because the EES, unlike previous alternatives to the MS, has a relatively clear theoretical structure (e.g., Laland et al. 2015) as well as a solid financial and institutional basis (Pennisi 2016; see also Fábregas-Tejeda and Vergara-Silva 2018a).

The debate between supporters of the EES and the MS is often characterized by communication failures and profound disagreements about crucial scientific issues: sometimes, they don't seem to understand each other very well, or, if they do, they nevertheless continue to have profound disagreements (e.g., Dickins and Rahman 2012; Mesoudi et al. 2013; Scott-Phillips et al. 2014; Gupta et al. 2017a, 2017b; Feldman et al. 2017; Welch 2017; Laland 2017; Uller and Helanterä 2019). A potential explanation for these disagreements and communication failures is (Kuhnian) incommensurability (Kuhn 1970 [1962]). Kuhn originally defined incommensurability as the lack of neutral standards from which to compare competing paradigms. This absence of a neutral basis would make it difficult for supporters of each paradigm to fully understand each other or to agree on important scientific issues, such as the preferred epistemic values to judge theories or the precise meaning of key terms.

The concept of incommensurability has been used by some philosophers of science to account for various scientific disputes throughout the history of science (e.g., Wray 2005, 2011; Chang 2013; Politi 2018). However, in the philosophy of biology there has been a reluctance to apply this and other Kuhnian concepts to disputes in evolutionary biology on the basis that Kuhn's account of scientific change does not work for fields and theories outside those from which it was originally developed, namely, the physical and astronomical sciences (Mayr 1994, 2004; notable exceptions to this have been Greene 1981; O'Malley and Boucher 2005; Pigliucci 2012). However, of late, some authors have vindicated the usefulness of Kuhn's ideas to shed light on some episodes of the history of evolutionary biology (Tanghe et al. 2018, 2021). This requires taking Kuhn seriously and not hastily rejecting what might be seen as a strawman depiction of his ideas.

In line with this resurgence of Kuhnian ideas in the philosophy of (evolutionary) biology, we suggest that the current dispute between the MS and the EES constitutes yet another episode amenable to a Kuhnian interpretation.

More specifically, we believe that the concept of incommensurability can account for the nature and characteristics of the dispute between advocates of the MS and the EES. Now, the application of the concept of incommensurability to this and other scientific controversies is not straightforward, given the different meanings and interpretations that Kuhn attached to this concept throughout his work. Thus, in order to successfully apply it to specific scientific disputes, it is necessary to discuss and make clear which of these different meanings and interpretations is being employed.

Recently, philosopher and evolutionary biologist Massimo Pigliucci (also one of the early proponents of the EES) attempted to determine whether the MS and the EES are incommensurable in a Kuhnian sense (Pigliucci 2017). After briefly analyzing the methods, semantics, and observational basis of each paradigm, Pigliucci concludes that there is no incommensurability between them. However, we posit that while valuable, his attempt is limited because when conducting his incommensurability analysis, he does not focus on the most contested parts of the debate.[1] In the present paper, we perform our own analysis of incommensurability, which seeks to overcome such a limitation. Unlike Pigliucci, we suggest that there are several pieces of evidence which suggest that there is incommensurability between the MS and the EES.

This paper is aimed at two audiences: Kuhn scholars who want to test Kuhn's ideas against particular scientific controversies and philosophers of biology who wish to make sense of the relationship between the MS and the EES. We would like to show the latter how Kuhn's concept of incommensurability, when properly considered, may shed light on this and other related scientific disputes in the biological sciences. Therefore, the structure of the paper is the

[1] For a full critique to Pigliucci's approach see Gefaell and Saborido (forthcoming).

following: in the first part, we introduce the MS versus EES debate. Secondly, we present the incommensurability thesis in Kuhn's work, discussing its changing meanings and interpretations. Thirdly, we try to establish whether the MS and the EES are in fact incommensurable. Finally, we briefly discuss three problems that derive from incommensurability as applied to this particular scientific controversy: that of the consequences of incommensurability, that of the mode of scientific change which better explains what is currently going on in evolutionary biology, and that of rational theory comparison.

2. What are the MS and the EES?

2.1. The Modern Synthesis

The MS was developed in the decades between 1920 and 1940 as a theoretical unification between a mathematical theory of natural selection and a population account of Mendelian genetics, through the work of Ronald A. Fisher, J. B. S. Haldane, and Sewall Wright. To this "synthesis", a series of disciplines—particularly taxonomy, botany, zoology and paleontology—were added by Theodosius Dobzhansky, Ernst Mayr, and other key figures, giving rise to the first grand unifying theory of modern biological science (e.g., Provine 1971, Mayr and Provine 1990, Smocovitis 1992, Bowler 2003).

From a theoretical point of view, the MS posits that evolution is the result of four evolutionary forces (mutation, migration, genetic drift, and natural selection) operating on the genetic composition of populations (Futuyma 2017). The MS focuses primarily on genes; evolutionary processes are explicitly defined as those that alter the genetic composition of populations, among which natural selection stands out as the only factor that can account for the fit between organisms and their environments (Scott-Phillips et al. 2014). Despite the fact that in the second half of the twentieth century several theoretical add-ons were incorporated into the MS, its structure as it is deployed in textbooks has barely changed over the years, and most evolutionary biologists are socialized into the discipline following the abovementioned theoretical tenets.

In addition to these theoretical tenets, two meta-scientific principles play a crucial role in the worldview of the MS. These are the "genetic program" metaphor and the "proximate/ultimate causation" dichotomy (e.g., Mayr 1961, 1998). According to the genetic program metaphor, the development of an organism is the result of the unfolding of a series of instructions coded in its genes and that have been shaped throughout evolutionary history by natural selection, genetic drift, and other evolutionary processes. In contrast, the proximate/ultimate causation dichotomy assumes that the immediate—*proximate*—factors that produce a particular phenotypic trait (i.e., its developmental and physiological basis) have nothing to do with the causes of its evolution (i.e., its *ultimate* causes), which include natural selection, genetic drift, and the other evolutionary processes.

2.2. The Extended Evolutionary Synthesis

Discontent over the limitations of the MS is an old phenomenon that dates back to the very inception of the MS. However, in its contemporary guise, the debate around the necessity of a new and "extended" evolutionary synthesis can be traced back to a series of publications by Massimo Pigliucci and theoretical and developmental biologist Gerd Müller (Pigliucci 2007; Müller 2007; Pigliucci and Müller 2010). These publications helped to set the terms of the discussion and sparked a debate between advocates and skeptics of this new EES (e.g., Dickins and Rahman 2012; Mesoudi et al. 2013; Laland et al. 2014). However, the debate definitely gained momentum through the work of Laland et al. (2015), who provided the first theoretical articulation of such an EES. For the purposes of our argument, henceforth we will follow the conception of the EES put forth by Laland et al. (2015)

Simply put, the EES rejects the MS's emphasis on genes and instead confers organisms a major role in evolution. Its supporters formalize this shift from genes to organisms into a relatively well-defined theoretical structure, which is made up of four scientific principles and two meta-scientific or ontological principles: the four scientific principles (called "biological background" by Laland and co-authors) are the main biological findings on which the EES is based. These include evolutionary developmental biology, developmental plasticity, inclusive inheritance, and niche construction. Additionally, two meta-scientific principles constitute the underlying assumptions that guide our understanding of the abovementioned scientific principles, and they encompass constructive development and reciprocal causation (Laland et al. 2015).

2.2.1. Scientific principles of EES

Broadly construed, evolutionary developmental biology (also known as evo-devo) refers to the study of the impact of developmental processes on evolution (Müller 2007). A common complaint against the MS is that it excluded developmental biology from the synthesis (e.g., Amundson 2005). For both theoretical and empirical reasons, the EES seeks to fully incorporate developmental biology into evolutionary biology (Laland et al. 2015; Walsh 2015). For this reason, evo-devo shapes much of the EES agenda and theoretical structure. In particular, supporters of the EES argue that evo-devo provides alternative explanations for well-known phenomena (such as, for instance, evolutionary convergence) that move away from business-as-usual explanations based on natural selection acting on random genetic mutations (Laland et al. 2015). These alternative explanations emphasize the role of internal developmental processes in generating adaptations (Müller 2007).

Developmental (i.e., phenotypic) plasticity is the ability of organisms to alter their phenotypes in response to environmental inputs (Laland et al. 2015). While phenotypic plasticity, understood as the outcome of standard evolutionary processes (particularly natural selection), is a well-established topic of study in the MS, supporters of the EES stress the importance of investigating this mechanism as a potential *cause*, rather than a mere *consequence*, of evolution.

Inclusive inheritance refers to an allegedly enlarged view of inheritance, in which parent–offspring resemblance is achieved through the intergenerational transfer of a diverse arrange of developmental resources which allow organisms to reconstruct their life cycles (Oyama et al. 2001; Laland et al. 2015; see also Uller and Helanterä 2017). Whereas the MS conceives inheritance as genetic transmission, proponents of the EES add several non-genetic mechanisms into the picture, including epigenetic tags, maternal effects, or ecological inheritance, that is, the altered environmental states resulting from parental activities (e.g., Danchin et al. 2011; Danchin and Pocheville 2014; Laland et al. 2015; Uller and Helanterä 2017; Jablonka 2017).

Finally, niche construction refers to the "process whereby the metabolism, activities and choices of organisms modify or stabilize environmental states" (Laland et al. 2015:4; see also Odling-Smee et al. 2003), thereby having an impact on the selective pressures that act on these and other organisms. Although both advocates and critics of the EES agree on the existence of niche construction, they disagree on the explanatory importance of such a concept (Scott-Phillips et al. 2014; Futuyma 2017; Gupta et al. 2017a, 2017b; Feldman et al. 2017; Uller and Helanterä 2019).

2.2.2. *Meta-scientific principles of EES*

Many novel concepts and empirical findings of the EES, by themselves, do not imply a radical break with the MS. However, proponents of the EES couple them with the meta-scientific—or ontological—principles of constructive development and reciprocal causation, which confer significantly different theoretical implications.

Constructive development refers to the "ability of an organism to shape its own developmental trajectory by constantly responding to, and altering, internal and external states" (Laland et al. 2015:6). Constructive development openly contrasts with the "genetic program" metaphor of the MS. Unlike this metaphor, constructive development does not grant genes a privileged role in developmental processes, and assumes that the various biological levels of organization can play a role in shaping the development of an organism. Reciprocal causation refers to a particular view of causes and effects in which "developing organisms are not solely products, but are also causes, of evolution" (Laland et al. 2015:6); this calls into question the "proximate/ultimate causation" dichotomy of the MS (Laland et al. 2011, 2013).

Taken together, the scientific and meta-scientific principles of the EES constitute a relatively well-defined theoretical structure that significantly departs from that of the MS, giving rise to frictions that, in our opinion, can be successfully analyzed using Kuhn's concept of incommensurability. However, before showing how incommensurability can shed light on the current dispute between advocates and critics of the EES, first we have to clarify what this concept amounts to and how to correctly interpret it.

3. Thomas S. Kuhn and the concept of incommensurability

Although Kuhn introduced the concept of incommensurability in *The Structure of Scientific Revolutions* (henceforth *SSR*), its precise meaning and interpretation changed throughout his career (Kuhn 1970 [1962], 1977a, 2000a [1981], 2000b [1982], 2000c [1990]; 2000d [1991], 2000e [1993]). Scholars such as Hoyningen-Huene (1990, 1993) have distinguished two different versions of incommensurability in Kuhn's works: (1) an early version, corresponding with that deployed in *SSR*, and (2) a later version, developed from *SSR* onward. In the following, we will discuss these different versions of incommensurability, contrasting them in a series of key points: What do they mean? What kinds of entities do they involve? And, when do they arise? Finally, we will discuss the merits of these different versions as well as which of them we should choose to analyze specific scientific disputes.

3.1. What is incommensurability?

In *SSR*, Kuhn defined incommensurability as the inexistence of a neutral ground from which to compare competing paradigms. Any attempt to evaluate their merits is made under the assumptions of one particular paradigm. This would lead to the inability of the proponents of each paradigm to "(…) make complete contact with each other's viewpoints" (Kuhn 1970:148).

In his post-*SSR* works, Kuhn defined incommensurability as the incapacity of point-by-point translation of competing theories (e.g., Kuhn 2000a, 2000b). According to Kuhn, point-by-point translation would fail due to the impossibility of transferring the taxonomic categories used in one theory to the other. These changes would provoke the breaking of the no-overlap principle of taxonomy, according to which a given object cannot belong to two categories simultaneously unless those two categories are related to each other in the same way that genera are related to species in biological taxonomy. This breaking of the no-overlap principle would cause, in turn, untranslatability. Because of its emphasis on taxonomic categories, some authors have called this post-*SSR* version of incommensurability "taxonomic incommensurability" (Sankey 1998).[2]

3.2. What does incommensurability involve?

In *SSR*, incommensurability is a process that involves *paradigms*, that is, all-encompassing frameworks that guide the research practices of scientists. Among other things, paradigms—or disciplinary matrices, as Kuhn would later call them—would help scientists set a research agenda, provide them with concepts and experimental tools to solve the problems that constitute such an agenda (i.e., "puzzles"), and give them a set of values with which to judge the merits of proposed solutions to such problems or puzzles (Kuhn 1970). In addition, paradigms supply scientists with a series of images or beliefs about how the world works and what its main constituents are. That is why according to Kuhn in *SSR*, incommensurability would have three domains: semantic, methodological, and observational incommensurability (Kuhn 1970; see also Hoyningen-Huene 1993; Hoyningen-Huene and Sankey 2001).

The first domain of incommensurability in *SSR* is semantic incommensurability. Kuhn states that both the old and the new paradigms involved in a scientific revolution share a lot of terms and experimental protocols,

[2] For a thorough discussion of taxonomic incommensurability see Hacking (1993).

but that they seldom use these elements in the same way, for "[w]ithin the new paradigm, old terms, concepts and experiments fall into new relationships one with the other." (Kuhn 1970:149) In other words, new paradigms give old concepts new meanings. This domain of incommensurability causes communication failures among proponents of each paradigm.

The second domain is methodological incommensurability, which refers to disagreements "(…) about the list of problems that any candidate for paradigm must resolve." (Kuhn 1970:148) Proponents of competing paradigms have different research agendas and prioritize different epistemic values when judging the validity of a solution to a given scientific problem (see also Kuhn 1977b).

The third and last domain of incommensurability in *SSR* has been called observational incommensurability (Bird 2018). Kuhn states that "(…) proponents of competing paradigms practice their trades in different worlds"; and because of that, "(…) the two groups of scientists see different things when they look from the same point in the same direction." (Kuhn 1970:150).

Interpretation of observational incommensurability is not straightforward, given Kuhn's ambiguities in this respect. Therefore, it is convenient to briefly discuss this matter before moving on. A first approach to Kuhn's presentation of observational incommensurability in *SSR* may lead us to think that Kuhn refers only to directly observable phenomena. According to this interpretation, Kuhn would consider observational incommensurability as a perceptual process through which directly observable entities and processes are perceived differently by proponents of each paradigm.[3] However, we believe

[3] By "directly observable" in this case we do not only mean those objects that can be seen with the naked eye, but also those that are observable through sense-amplifying devices, such as microscopes or telescopes.

that a more plausible interpretation is that, by observational incommensurability, Kuhn is referring to the ontological—or metaphysical—beliefs that underlie the interpretation of phenomena in different paradigms. For example, the main example with which Kuhn illustrates observational incommensurability in *SSR* has to do with to the different conceptions of space that underlie Newtonian and relativistic physics, conceptions that respectively derive from Euclidean and Riemannian geometries. Kuhn points out that certain scientists—Newtonians—are "(...) embedded in a flat [space]", while others—the Einsteinians—inhabit "(...) a curved, matrix of space" (Kuhn 1970:150). The "matrix of space" is not something that can be perceived directly; quite the contrary, it refers to a broad-ranging ontological assumption that guides the interpretation of observable phenomena in a given paradigm and tells its scientists what kinds of entities and processes populate the world. So, we believe that this view of observational incommensurability as the set of ontological assumptions of paradigms is the most adequate interpretation of said domain of incommensurability. Therefore, henceforth we are going to refer to it as "ontological incommensurability".[4]

In his post-*SSR* writings, Kuhn abandoned the concept of paradigm due to frequent misunderstanding and misappropriation, and instead began to talk about "theories" understood as purely linguistic constructs (that is why some Kuhn scholars have talked about a "linguistic turn" following *SSR*; Irzik and Grünberg 1998; Bird 2002). Therefore, in this second phase, Kuhn reframed

[4] This particular interpretation of observational incommensurability as ontological assumptions is also in line with Alexander Bird's connectionist account of observational incommensurability, according to which "a person's 'world' (…) is made up not of their perceptions and language, but (also) of the quasi-intuitive associations they make, the learned similarities and associations that channel our thoughts in one direction rather than another" (Bird 2002:450). According to Bird, "[w]hat differs between scientists is not their perceptual experiences, but what those experiences intuitively, (second-)naturally and rule-lessly prompt then to think and say." (Bird 2002:450). In other words, what differs between scientists from different paradigms are the ontological assumptions that (spontaneously) guide their interpretation of phenomena and tell them what kinds of entities and processes exist in the world.

incommensurability as a completely linguistic phenomenon that affects the meaning of certain subsets of terms of competing theories.

3.3. When does incommensurability arise?

In *SSR*, Kuhn understood incommensurability as applied to "classical" scientific revolutions, that is, those episodes in which the old paradigm is replaced by a new one that solves some of the anomalies that drove the revolution in the first place.

However, in his post-*SSR* writings (especially those of the 1990s), Kuhn argued that the most frequent kind of scientific change would be scientific specialization, that is, the emergence of new scientific disciplines (Kuhn 2000c, 2000d, 2000e; see also Wray 2005, 2011; Politi 2017, 2019). These new scientific disciplines would emerge when a small group of scientists from a given scientific community devote significant time and energy to solve problems to which the rest of the community does not pay attention. To solve these problems, this group of scientists may come up with new (and sometimes heterodox) concepts and methods, some of which may help resolve at least some of the problems. Resolved problems may eventually lead to the discovery of new unexpected phenomena, or to the formulation of new and unexpected scientific problems. On those occasions, this initially small part of the scientific community may definitively separate from the rest of their peers, leading to the emergence of a new scientific community that focuses only on these new problems (see Politi 2019). The definitive branching off of this group of scientists may further increase the divergence in methods, concepts and agenda between them and the original community.

In this post-*SSR* phase, for Kuhn, incommensurability would act as the isolation mechanism between the two scientific communities that have been separated as a result of specialization. According to his view, the newly created scientific community would make use of different taxonomic categories, which in turn would provoke the breaking of the no-overlap principle and would impede "effective" or "full" communication with the original scientific community (Kuhn 2000d; see also Wray 2005, 2011).

3.4. Incommensurability: which version to choose?

> To sum up, throughout Kuhn's work it is possible to distinguish between two versions of the incommensurability thesis: for the *SSR* version, incommensurability refers to the inexistence of a neutral ground from which to compare competing paradigms; it involves the semantic, methodological, and ontological domains of such paradigms, and it arises during paradigm-shifting revolutions. In contrast, in the taxonomic, post-*SSR* version, incommensurability is defined as the incapacity of point-by-point translation of theories; it involves certain subsets of terms of such theories, and arises during processes of scientific specialization (see table 1).

[INSERT TABLE 1 ABOUT HERE]

These differences between the *SSR* and post-*SSR* versions of incommensurability raise the problem of which one of them is more adequate to analyze specific scientific disputes. In order to answer this question, let's take a look at the recent incommensurability literature.

Let's begin with the post-*SSR*, taxonomic version of incommensurability. Despite being Kuhn's most developed version, in recent times, taxonomic incommensurability has been the subject of extensive discussion among Kuhn scholars. Fundamentally, there have been disagreements as to how to correctly interpret the concept. For instance, Wang (2002) has claimed that taxonomic incommensurability has more to do with logic than with meanings, and Politi (2020) argues that Kuhn's late notion of incommensurability was not about taxonomies and that, contrary to the most popular interpretation, he never underwent a linguistic turn. Additionally, Kuhn scholars have diverged over the merits of taxonomic incommensurability: some authors have defended it (e.g., Andersen et al. 2006; Wray 2007), while others have criticized it (most notably, Mizrahi 2015). Particularly compelling is the argument put forward by Bird (2012) against taxonomic incommensurability, suggesting that as not all scientific theories have a taxonomic structure, incommensurability cannot be strictly taxonomic in nature.

While the post-*SSR*, taxonomic version of incommensurability has been criticized by various Kuhn scholars, a growing number of authors have recently vindicated the value of the *SSR* version of incommensurability, suggesting that despite being formulated in a more imprecise fashion, it is a much richer concept (Richardson 2002; Politi 2018). This richness stems from the consideration it gives to methodological and ontological issues in scientific disputes. Consistent with this assessment, several authors have called for a "back to *Structure*", as Chang (2013:171) has put it; that is, a return to engaging with the methodological and ontological aspects of scientific controversies. For instance, Chang himself has proposed the view that the Chemical Revolution was more about methodological than semantic incommensurability (Chang 2013). Samir Okasha (2011) has also recently discussed methodological incommensurability, and Bird (2005, 2008) has proposed a connectionist interpretation of observational (i.e., ontological) incommensurability. In sum, a growing number of Kuhn scholars have questioned the taxonomic, post-*SSR* version of incommensurability, while having begun to engage with the different domains of the *SSR* version of incommensurability.

We sympathize with this trend; in particular, we believe that the *SSR* version of incommensurability is more adequate in the analysis of scientific disputes because the underlying conception of science that it involves—that of a practice conducted under the auspice of a paradigm or disciplinary matrix—better captures the nature of science. We feel it is quite misleading to reduce the whole scientific enterprise to the semantic properties of its theories, as the post-*SSR* version of incommensurability does. Science is a complex thing that involves methods, values, and ontological assumptions—that is, practical issues—alongside theories and concepts, and this characterization of science is more in line with paradigms and the *SSR* version of incommensurability than with Kuhn's post-*SSR* works. In this sense, we totally agree with W. H. Newton Smith when he points out that:

> The positive and salutary virtue of Kuhn's use of his notion of a paradigm is to remind us that in looking at the scientific enterprise it is important to focus on more than the theories (in the narrow sense of the term) advocated within a given community. (…) For, in general, it directs our attention to the fact that in understanding the scientific enterprise we must look not only at theories proper but also at a wider range of beliefs, attitudes, procedures and techniques of the scientific community. (Newton-Smith 1981:106-107)

If science is defined only in terms of its semantic or taxonomic properties, then perspective is lost about the causes of many scientific conflicts that lie behind the daily work of scientists—related to practical issues, such as the different experimental protocols they employ, the different metaphors and ontological beliefs they use as background assumptions for research, or the different epistemic values they hold. To lay aside these practical aspects of science is to lay aside a crucial part of its nature.[5]

In short, we believe that the *SSR* version of incommensurability is best suited to the analysis of scientific controversies because of its reliance on the paradigm concept, which confers a great deal of importance on practical issues. However, this does not mean that some ideas originally attached to the post-*SSR* version of incommensurability cannot be taken into account when conducting incommensurability analysis. In particular, we maintain that a commitment to the *SSR* version of incommensurability does not force us to accept the view that this phenomenon only takes place in paradigm-shifting revolutions. Instead, we believe that the *SSR* version of incommensurability can be compatible either with a paradigm-shifting revolution or a process of scientific specialization.

4. Incommensurability and the MS versus EES debate

Now that we have already introduced the MS and the EES, and have briefly discussed the precise meaning and interpretations of the concept of incommensurability, in this section we'll try to determine whether the MS and the EES are incommensurable according to the *SSR* version of incommensurability. For this, we'll assume that both the MS and the EES can be

[5] For a reinterpretation of Kuhn's ideas in terms of a philosophy of scientific practice see Rouse (2003, 2013).

considered Kuhnian paradigms and we will proceed according to the different domains of incommensurability in the *SSR* version: semantics, methodology, and ontology.

4.1. Semantic incommensurability in the MS versus EES debate

Some authors involved in the dispute have already acknowledged that communication failures often take place between supporters of the MS and the EES (Uller and Helanterä 2019). To a large extent, these communication failures are caused by the different meanings attached to key terms in the MS and the EES. For example, the very meaning of "evolution" varies significantly between the MS and the EES. The MS tends to define evolution as "changes in gene frequencies" (Dobhzansky 1937; Futuyma 2005; Herron and Freeman 2014), while the EES does so as "transgenerational change in the distribution of heritable traits of a population" (Laland et al. 2015:2).[6]

Other concepts crucial to any evolutionary theory such as "inheritance" are also conceived quite differently in the MS and the EES. In section 2.2.1. we pointed out that the MS conceives inheritance as genetic transmission, whereas advocates of the EES do not establish a close link between genes and heredity in order to make room for non-genetic mechanisms as relevant causal factors in inheritance (Jablonka and Lamb 2005; Danchin et al. 2011; Danchin and

[6] It is worth noting that in a recent publication, Douglas J. Futuyma, a classic figure in the MS movement, defines evolution in a similar fashion, as change in "the frequency of heritable variations within populations, from generation to generation" (2017:2). However, he quickly adds that heritable variations are based on genes, thus approaching the classical conception of evolution and moving away from that of supporters of the EES. In a similar vein, in the last edition of Futuyma's *Evolution* (Futuyma and Kirkpatrick 2017), their authors define evolution as the "inherited change in the properties of groups of organisms over the course of generations". Nevertheless, when they refer to the causes of evolution in "current theory of evolution", they only mention classic mechanisms such as mutation, recombination, gene flow, isolation, genetic drift, and natural selection (Futuyma and Kirkpatrick 2017:8), most of which refer to genetic processes.

Pocheville 2014; Laland et al. 2015; Uller and Helanterä 2017; Jablonka 2017).[7] We suggest that these semantic changes can also be interpreted as instances of semantic incommensurability.

Some may object that these semantic changes do not amount to incommensurability, given that the EES notion of inheritance is no more than an *extension* of that of MS. However, we believe that there is at least one reason to be skeptical of this interpretation, and it is that the EES concept of inheritance implies the abandonment of certain cherished ontological assumptions of the MS, particularly those of the proximate/ultimate causation dichotomy and the genetic program metaphor (Laland et al. 2015; Uller and Helanterä 2017). Given that inheritance as understood by the EES is difficult to reconcile with such ontological assumptions, the "extension" interpretation is hard to sustain. These conceptual changes appear to be more profound, and we suggest they can count as instances of semantic incommensurability.

4.2. Methodological incommensurability in the MS versus EES debate

An analysis of the disputes between advocates of the MS and the EES reveals that these usually stem from profound disagreements over the kinds of problems that each camp considers to be worth resolving, their different explanatory preferences, their divergent ranking of epistemic values, or even their opposed views about the desirable status of evolutionary biology as a scientific discipline (e.g., Scott-Phillips et al. 2014; Laland et al. 2015; Müller 2017; Futuyma 2017), something which points to methodological incommensurability.

Let's look at some examples in more detail. Take, for example, disagreements over the kinds of problems that are worth solving. Due to its

[7] That is why some EES-friendly authors have advocated for a pre-MS notion of inheritance, conceived as the pattern of resemblance between parents and offspring (Walsh 2015).

emphasis on genes, the theoretical backbone of the MS is based on the discipline of population genetics, which largely determines the kinds of problems and solutions that evolutionary biologists pursue in their daily work (Dobzhansky 1937; Ridley 2003; Freeman and Herron 2004; Futuyma 2005; Lynch 2007). We believe that most supporters of the MS agree with Theodosius Dobzhansky's classic statement that "(…) the mechanisms of evolution constitute problems of population genetics." (Dobzhansky 1937:11-12), and indeed some contemporary authors have vindicated the importance of population genetics for evolutionary biology (Lynch 2007). In contrast, advocates of the EES do not grant population genetics such importance. Instead, they would probably agree with EES-friendly developmental biologist Scott Gilbert and collaborators, who as early as 1996 claimed that "[p]opulation genetics is destined to change if it is not to become as irrelevant to evolution as Newtonian mechanics is to contemporary physics" (Gilbert et al. 1996:368). Because of this, problems committed to a population genetics approach such as, for instance, accurately estimating the effective census of a population (*Ne*) or inferring the role of natural selection on phenotypic traits based on Q_{ST}-F_{ST} comparisons—to name two typical problems under a MS approach—are pretty much absent from the EES agenda. In contrast, scientists of the EES are much more focused on problems related to developmental biology, such as the role of developmental plasticity in evolutionary innovations.[8]

The importance attached to developmental processes in the EES involves not only new topics of research, but also the use of new model organisms that are much less used in the MS but that are extremely useful to the study of developmental processes, such as the dung beetles from the genus *Ontophagus* (e.g., Casasa and Moczek 2018; Baedke et al. 2020). This choice of different model

[8] For a full description of the research agenda of the EES see: https://extendedevolutionarysynthesis.com/the-project/research-projects/

organisms, in turn, "(…) make[s] it harder to align their data and methodologies with those of SET [i.e., MES]." (Baedke et al. 2020:18).

Another example of methodological incommensurability between the MS and the EES has to do with explanatory preferences, or the kinds of properties a given paradigm prioritizes as explanations for phenomena (e.g., Müller and Newman 2005; Müller 2007, 2017; Craig 2010; Pigliucci and Müller 2010; Fábregas-Tejeda and Vergara-Silva 2018b). Supporters of the MS prefer what Peter Godfrey-Smith has called "explanatory externalism", that is, "explanations of properties of organic systems in terms of properties of their environments" (Godfrey-Smith 1996:30). Indeed, supporters of the MS favor explanations based on the dynamics of genes in populations (migration, genetic drift) paired with external selective pressures. The internal dynamics of organisms hardly have a place in the *explanans* of evolutionary theory for supporters of the MS. In contrast, the EES approach:

> (…) moves the focus of evolutionary explanation from the external and contingent to the internal and inherent. It posits that the causal basis for phenotypic form resides not in population dynamics or, for that matter, in molecular evolution, but instead in the inherent properties of evolving developmental systems. (Müller 2007:947-948)

In other words, the EES is committed to explanatory internalism, or the belief in "[e]xplanations of one set of organic properties [in this case, the ability to undergo evolution through generations] in terms of other internal or intrinsic properties of the organic system" (Godfrey-Smith 1996:30). The role conferred on developmental processes, plasticity or agentic behaviors by advocates of the EES testifies to their commitment to explanatory internalism, thus moving away from the explanatory externalism of the MS.

Methodological incommensurability also exists in relation to epistemic values (Baedke et al. 2020). There are several examples of advocates of the MS and the EES disagreeing about which epistemic values they should prioritize when judging the merits of their theories and hypotheses (Scott-Phillips et al. 2014; Müller 2017; Futuyma 2017). For instance, in an interesting paper that contrasts the views of the MS and the EES on niche construction, advocates and critics alike agree that "these two accounts [the MS and the EES] differ more in terms of style of explanation [i.e., epistemic values] than dissimilarities in empirical findings or predictions" (Scott-Phillips et al. 2014:1234). Advocates of the EES acknowledge that niche construction does not make any new predictions that, in principle, could not be made with the MS (Scott-Phillips et al. 2014). However, unlike their counterparts from the MS, they seem to confer predictive power a lower epistemic status than other epistemic values in which niche construction allegedly stands out, such as heuristic power or the ability to generate new perspectives from which to approach well-known phenomena (Scott-Phillips et al. 2014:1238). In contrast, it appears that, for supporters of the MS, predictive power is a highly ranked epistemic value. According to their criteria, there is no need for a new paradigm if it is as predictive as the old one and both can satisfactorily account for the same phenomena (Scott-Phillips et al. 2014).

Another epistemic value about which advocates of the MS and the EES seem to disagree is simplicity. It seems that advocates of the MS tend to confer simplicity a high epistemic rank: "Simpler explanations are generally preferred over more complex (and vague) hypotheses, unless these are supported by evidence" (Futuyma 2017:8). For them, the simpler a theory, the better. Conversely, advocates of the EES usually deem explanations of the MS as "too simple" or "impoverished" (Scott-Phillips et al. 2014:1236, 1240), suggesting that they do not regard simplicity as of such importance as supporters of the MS. Instead, they tend to prefer less idealized explanations, even if they involve multiplying the number of causal factors in explanations or not incorporating as many simplifying assumptions as the models of the MS (Baedke et al. 2020).

One last example of methodological incommensurability between the MS and the EES has to do with the desirable status of evolutionary biology as a science, and the best way to ensure scientific progress (Uller and Helanterä 2019). Advocates of the EES are staunch defenders of scientific pluralism, which we can see in the following two examples: "We believe that a plurality of perspectives in science encourages development of alternative hypotheses, and stimulates empirical work" (Laland et al. 2014:164); "We believe that a plurality of perspectives in science is healthy (…)" (Laland et al. 2015:10; see also Laland 2018). In contrast, supporters of the MS, with their insistence that their paradigm can satisfactorily account for most new biological phenomena, suggest that they view scientific progress as driven more by theoretical unification than by scientific pluralism.[9]

4.3. Ontological incommensurability in the MS versus EES debate

While it is certainly true that most of the "brute" facts are shared between the MS and the EES, their supporters interpret them under a significantly different light. In fact, advocates of the EES have been quite explicit in their ontological assumptions, as we have seen in section 2.2 (Laland et al. 2015). There

[9] In fact, the MS itself was described by its founders as a clear example of theoretical unification (e.g., Mayr and Provine 1990). This spirit of unification seems to be shared by their descendants.

are at least three examples of ontological incommensurability between the MS and the EES: the nature of organisms, the organism-environment relationship, and evolutionary causation.

The conception of organisms under the MS and the EES is quite different. Although this point has been contentious for the supporters of the MS themselves (see for example Mayr 2001; also Depew 2011, for a discussion of Dobzhansky's views), most of them tend to conceive organisms as "vehicles" of their genes, which are considered ultimate targets of selection in many of their population genetics models. This view was originally presented by George Williams (1966) and later developed by scientists such as Richard Dawkins (1976) and philosophers such as David Hull (1980). Under this view, ontological primacy in evolution is granted to genes.[10] Conversely, proponents of the EES view organisms as holistic and autonomous entities. They reject the claim that organisms are merely "vehicles" of genes (Noble 2011), and instead view organisms as integrated wholes (Walsh 2015). Advocates of the EES have no qualms about attributing agency to organisms, while most proponents of the MS conceive them in a mechanical way, as an epiphenomenon of molecular processes (Dawkins 1976). Given their emphasis on organisms, it is no coincidence that some EES-friendly philosophers of biology have championed the resurgence of organicism in the biological sciences (e.g., Huneman 2010; Walsh 2015; Huneman and Walsh 2017).

[10] Futuyma (2017:9) has protested this depiction of the MS, insisting that its founders were interested in organisms as a whole. However, he readily points out that these authors realized that for the properties of organisms to evolve, they have to be inherited. But, since for the MS only genes are passed down through generations, it means that the fundamental entities of evolution remain the genes themselves. Even those MS biologists more sympathetic to organicism did not substantially alter their view of evolution to put organisms at the forefront. For instance, Ernst Mayr, who thought that organisms are the target of selection and criticized "bean-bag genetics", also understood organisms as being the result of the unfolding of a genetic program (Mayr 1998), which again confers genes a privileged role.

The second example of ontological incommensurability between the MS and the EES involves the relationship between organisms and their environment (Lewontin 2002; Odling-Smee et al. 2003; Scott-Phillips et al. 2014). The role of niche construction in evolutionary models of the EES suggests that its advocates understand organisms and their environment as entangled entities, with much blurrier boundaries than assumed in the MS. In the EES, organisms are not independent from the environment, and the latter is partially constructed by the agentic and non-agentic actions of the former. This means that the fit between organisms and their environments is achieved concurrently by natural selection and niche construction (Odling-Smee et al. 2003; Laland et al. 2015; Laland and Chiu 2021). This contrasts with the organism–environment relationship in the MS, which can be clearly illustrated with the concept of "environmental niche" (Walsh 2015). An environmental niche is defined as the particular set of physiochemical parameters of the environment to which organisms must adapt in order to survive and reproduce. According to the MS, environmental niches are ontologically independent and predate the existence of organisms, which adapt to environmental niches in a passive way, through natural selection acting on random mutations.

The third and final example of ontological incommensurability between the MS and the EES has to do with evolutionary causality (e.g., Laland et al. 2011, 2013; Noble 2012; Martínez and Esposito 2014; Fábregas-Tejeda and Vergara-Silva 2018b; Uller and Helanterä 2019). At the heart of this divergence is the status of the "proximate/ultimate causation" dichotomy (Mayr 1961). According to Laland and colleagues, it seems that this dichotomy "(…) has acted like a meta-theoretical conceptual framework to stabilize the dominant scientific paradigm" (Laland et al. 2011:1516; see also Fábregas-Tejeda and Vergara-Silva 2018b); or, in other words, has stabilized the MS. Indeed, supporters of the MS are sometimes skeptical of the EES because they consider that their models confound the proximate and ultimate causes of biological traits (Dickins and Rahman 2012, Futuyma 2017). For instance, they believe that evo-devo does not significantly challenge the MS because it only deals with the proximate causes of traits, and not with their ultimate causes (Futuyma 2017). Something similar occurs with epigenetic inheritance: advocates of the MS have accused those of the EES of confusing proximate and ultimate causes when discussing the role of non-genetic mechanisms in evolution (Dickins and Rahman 2012).

In contrast, supporters of the EES reject the proximate/ultimate dichotomy, and believe that some processes traditionally considered proximate causes (including those studied by evo-devo, or those dealing with non-genetic inheritance) are actually evolutionary causes or have a decisive contribution to these (Laland et al. 2011, 2013, 2015). Unlike their MS counterparts, advocates of the EES believe that inheritance, variation, and differential fitness are intertwined processes (Walsh 2015; Uller and Helanterä 2019), and that causality goes both up and down through the biological levels of organization (Martínez and Esposito 2014; Laland et al. 2015). For them, cells and tissues can cause changes in the activity of genes in the same way as these can cause changes in the activities of cells and tissues. This, in turn, implies a commitment to the notion of downward causation (Campbell 1974), which is completely absent from the MS worldview and that has been the subject of much philosophical discussion due to the difficulty of fitting it into a naturalist framework (e.g., Flack 2017).

[INSERT TABLE 2 ABOUT HERE]

5. Implications of incommensurability between the MS and the EES

Our conclusion, therefore, is that there is incommensurability between the MS and the EES in the semantic, methodological, and ontological domains. This poses at least three problems: that of the consequences of incommensurability, that of the mode of scientific change, and that of rational theory comparison.

5.1. The consequences of incommensurability: communication failures or profound disagreements?

What effects does incommensurability have on the participants in this dispute? Does it provoke unsolvable communication failures or profound disagreements? Kuhn suggested that incommensurability would impede full communication between scientists from different paradigms (Kuhn 1970, 2000d). Was Kuhn right about this? We suggest that, contrary to what Kuhn argued, the main consequences of incommensurability are not communication failures but profound disagreements, that is, disagreements that cannot be solved by appeal to empirical data alone.

We do not deny that between supporters of the MS and the EES there exist communication failures: as we have seen, these take place in the semantic and ontological domains. However, we suggest that these communication failures are solved relatively easy. In order to show why, let's introduce Chang's distinction between the three different levels of scientific discourses: operational, phenomenal, and theoretical (Chang 2013:160). The operational level refers to descriptions of experimental procedures, such as those that take place in laboratories. The phenomenal level refers to immediate descriptions of the observable properties of the objects of study. Finally, the theoretical level refers to those descriptions or interpretations of phenomena in terms of theoretical entities and processes.

Chang (2013) has argued that although semantic incommensurability played a role in the Chemical Revolution, it did not pose a radical challenge to communication between advocates of the oxygen and phlogiston paradigms because it only affected the theoretical level, leaving the operational and phenomenal ones fully commensurable. Although communication failures did occur between proponents of each paradigm, these were solved relatively easily by appeal to the operational and phenomenal levels. We suggest the same is true for advocates of the MS and the EES: although at first the proponents of both paradigms experience communication failures due to semantic and ontological incommensurability, these are solved when they abandon the theoretical level and begin to focus on the operational and phenomenal levels of discourse.

So, it seems that the incommensurability between MS and EES does not lead to unsolvable communication failures. The really pressing problem is that when the communication failures between the proponents of the MS and the EES are solved, significant disagreements persist between them regarding several methodological and ontological issues. Contrary to what may appear at first glance, methodological and ontological incommensurability do not cause communication failures between proponents of the MS and the EES. The analysis of their disputes shows that both parties understand each other quite well most of the time, and when they do not, they can appeal to the operational and observational levels of discourse to clarify their positions. Rather than a complete failure in communication, most of the time, methodological and ontological incommensurability provokes deep disagreements on various issues—such as which epistemic values should be prioritized when evaluating scientific hypotheses, or what is the real nature of causation in evolutionary processes. These differences are hard to solve, since they involve deeply engrained ontological and normative beliefs about which kinds of entities and processes exist in the world and how good science should be conducted.

In sum, we believe that Kuhn missed the mark when he argued that communication failures, and not profound disagreements, are the main consequence of incommensurability.

5.2. What is currently going on in evolutionary biology? A rational reconstruction proposal

If the MS and the EES are incommensurable, what kind of scientific change is currently taking place in evolutionary biology? Is it a paradigm shift, or is it a process of scientific specialization? At first glance, the response to this question would seem to be the former, given that in our analysis of the MS versus EES controversy we employed the *SSR* version of incommensurability, which entails paradigm-shifting revolutions. However, this is not necessarily the case: as we argued at the end of section 3.4, it is also possible to make the *SSR* version of incommensurability compatible with a process of scientific specialization. Therefore, we now have to determine which mode of scientific change (paradigm shift or scientific specialization) better explains the current situation.

In order to asses this question, let's lay out our vision of what has happened in evolutionary biology over the last few decades. We suggest that throughout the second half of the twentieth century, a number of discoveries were made in the biological sciences which suggested that some ontological assumptions of the MS (such as the genetic program metaphor or the proximate/ultimate causation dichotomy) were wrong, and also drew attention to some processes that, although having been studied under the MS umbrella, were not given enough consideration (i.e., niche construction). This triggered the development of a new view of evolution in which organisms play a central role; this new view of evolution stimulated the redefinition of key concepts, and prompted a new research agenda based on these new ontological assumptions and their concomitant methodological prescriptions. Once this view of evolution was vindicated by enough authors, social and institutional mechanisms began to play a role, and the EES community started to organize itself (see figure 1).[11]

[INSERT FIGURE 1 ABOUT HERE]

Given such a scenario, are we witnessing a paradigm shift or the emergence of a new scientific specialty? We incline towards the latter option, albeit with reservations. Our main argument for the scientific specialization hypothesis is that advocates of the EES have repeatedly stated that they do not want to replace the MS, but only to work independently of it, turning evolutionary biology into a plural science (Laland et al. 2015; Laland 2018). This may end up isolating the scientific community of the EES from that of the MS given their ontological and methodological disagreements. However, although plausible, for the moment we find it hard to imagine that the MS versus EES dispute will end by giving rise to two separate specialties, given that advocates of each camp consider themselves as evolutionary biologists *tout court* (and not members of a particular specialty within evolutionary biology), and that both

[11] Some authors have suggested that the emergence of the EES can be explained by social or extra-scientific factors (e.g., Gupta et al. 2017; Welch 2017; Futuyma 2017). We do not agree: although we do not deny that such processes may have played a part, we believe that the reasons for the emergence of the EES are mainly epistemic, something which is in line with Kuhn's own view and also that of most Kuhn scholars (e.g., Wray 2005, 2011; Politi 2019).

paradigms sometimes compete for the explanation of the same phenomena (such as, for instance, those pertaining to niche construction; Scott-Phillips et al. 2014). Taking this into account, we should not definitively rule out the possibility of a paradigm shift in the medium term.

5.3. Rational theory comparison and incommensurability between the MS and the EES

A third and final problem that emerges from our analysis of incommensurability is that of rational theory comparison. If the MS and the EES are incommensurable, does it mean that they cannot be rationally compared? Kuhn insisted throughout his career that incommensurability does not preclude rational theory comparison, as long as we assume a weaker version of rationality than that of the logical positivists, who conceived of it as a quasi-mechanical ability (Kuhn 1977b, 2000b). So, how can we rationally compare the MS and the EES?

One possibility is to look at the evidence supporting each paradigm in order to determine which of them fares better in this regard. This strategy should be prioritized when possible, but it does not guarantee success. The fact that scientists from both camps agree that the MS and the EES differ more in "style of explanation" [i.e., epistemic values] than in empirical findings (Scott-Phillips et al. 2014:1234) points to underdetermination of theories by data, suggesting that data alone cannot solve the differences between proponents of each paradigm.

Incommensurability poses two problems for the rational comparison of the MS and the EES: disagreements regarding the ranking of epistemic values, and disagreements regarding ontological assumptions. Therefore, efforts should be focused on tackling these problems. Disagreements on the ranking of epistemic values could be reduced by performing agreed evaluations of each paradigm according to broadly shared epistemic values, in a sort of epistemic adversarial collaboration. If there is a possibility of evaluating which paradigm works best in relation to given shared epistemic values (e.g., simplicity or heuristic power), that might be a starting point for a rational comparison of the MS and the EES. That would not eliminate incommensurability—which has to do with differences in the *ranking* of such shared epistemic values—but it could certainly tighten the gap between both camps. Recent attempts at epistemic evaluation of the MS and the EES, such as that of Baedke et al. (2020), are an invaluable first step in that direction.

Alternatively, disagreements regarding ontological assumptions could be addressed if scientists from each paradigm engage in philosophical discussions about the merits and limitations of the different ontological assumptions of each paradigm. As we have seen in section 4.3, many controversies between advocates of the MS and the EES have to do with ontological issues. Since ontology is a branch of philosophy, these controversies must be addressed with the help of philosophical tools. For this reason, we believe that a rational comparison of the MS and the EES would be easier if their advocates conscientiously engaged in philosophical discussions about the merits of the genetic program metaphor, downward causation, or constructive development, among other controversial ontological assumptions of either the MS or the EES. Of course, we are not suggesting that evolutionary biologists must become philosophers, but only that, along with empirical data, they should take more into account the philosophical aspects surrounding their scientific disputes.[12]

[12] In this regard, nowadays advocates of the EES certainly outperform those of the MS, since they confer philosophical reasoning a much more important role in their theorizing than their scientific rivals from the MS (see, for instance, in Uller and Laland 2019).

6. Conclusion

In this paper we have vindicated the value of the *SSR* version of incommensurability for analyzing scientific disputes. We have argued that there is incommensurability between the MS and the EES, and we have suggested that the main consequence of this incommensurability is the emergence of profound disagreements between the advocates of each paradigm. We also hold that the scientific change that is currently taking place in evolutionary biology is more akin to a process of scientific specialization than to a paradigm-shifting revolution. Finally, we have discussed some problems of incommensurability for rational comparison between the MS and the EES, and have proposed two solutions to help in this task. One final point to consider is the following: Kuhn's ideas are often reviled for not being valid in accounting for the various characteristics of science (and, particularly, evolutionary biology), and calls are made to not settle for worn-out and ready-made solutions (see Fábregas-Tejeda and Vergara-Silva 2018a). These calls are not without merit, since Kuhn's model has several widely known limitations. However, we believe that prior to making any general judgment regarding Kuhn's ideas, we must evaluate each of them separately in particular contexts in order to determine which one may be of most value and which one of them we must abandon altogether. A priori judgements are not very rewarding. In other words, before committing to or denigrating Kuhn, we have to take him (more) seriously.

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Table 1. A summary of the different versions of incommensurability in Kuhn's works.

Version of incommensurability	**What does it mean?**	**What does it involve?**	**When does it arise?**
SSR	Inexistence of a neutral ground from which to compare competing paradigms	Semantic, methodological, and ontological domains of competing paradigms	During paradigm-shifting revolutions
Post-*SSR*	Incapacity of point-by-point translation of theories due to the breaking of the no-overlap principle	Subsets of terms of competing theories	During processes of scientific specialization

Table 2. A summary of incommensurability (understood in a *SSR* fashion) between the MS and the EES.

Domain of incommensurability	**Modern Synthesis (MS)**	**Extended Evolutionary Synthesis (EES)**	**Consequences**	**References (selected)**
Concepts	Evolution as changes in allele frequencies; inheritance as genetic transmission	Evolution as changes in the heritable composition of populations; inheritance as transgenerational resemblance or transfer of developmental resources	Occasional communication failures, but solvable	Laland et al. (2015); Walsh (2015); Uller & Helanterä (2017)
Methodogy	Population genetics agenda; classic model organisms; explanatory externalism; predictive power, simplicity; unified science	Developmental agenda; non-model organisms; explanatory internalism; heuristic power, new perspectives; epistemic pluralism	Profound disagreements over methodological and epistemic issues; no communication failures	Müller (2007, 2017); Scott-Phillips et al. (2014); Futuyma (2017); Uller and Helantera (2019); Baedke et al. (2020)
Ontology	Genecentrism; mechanicism; proximate/ultimate dichotomy; organism-environment independence; bottom-up causality	Organicism; agency; rejection of proximate/ultimate dichotomy; environment-organism entanglement; multilevel causality	Occasional communication failures, but solvable; profound disagreements over the nature of organisms, the organism-environment relationship and evolutionary causation	Futuyma (2017); Dikins and Rahman (2012); Laland et al. (2011, 2013); Noble (2012); Martínez and Esposito (2014); Uller and Helantera (2019)

Figure 1. Schematic representation of the rational reconstruction of the history of evolutionary biology during the last decades. This view shares some elements with that of Otsuka (2019), who confers ontological assumptions and beliefs a great deal of importance for configuring a conceptual framework.