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Misconceptions, conceptual pluralism, and conceptual toolkits: bringing the philosophy of science to the teaching of evolution

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Abstract
This paper explores how work in the philosophy of science can be used when teaching scientific content to science students and when training future science teachers. I examine the debate on the concept of fitness in biology and in the philosophy of biology to show how conceptual pluralism constitutes a problem for the conceptual change model, and how philosophical work on conceptual clarification can be used to address that problem. The case of fitness exemplifies how the philosophy of science offers tools to resolve teaching difficulties and make the teaching of scientific concepts more adequate to the actual state of affairs in science.

Keywords Conceptual change · Conceptual pluralism · Conceptual toolkit · Fitness · Natural selection

1 Introduction: conceptual change and its critics

The literature in science education has long focused on a conceptual change model for the teaching of scientific concepts.[1] While there are many versions of the general conceptual change model, all start by rejecting the view that students

[1] Early statements of the model include Posner et al. (1982), Strike & Posner (1982) and Carey (1985). Hewson (1992), Duit et al. (2008), DiSessa (2014), Nehm & Kampourakis (2016) and Vosniadou (2019) provide excellent overviews of the considerable diversity of views among researchers and practitioners in science education of what conceptual change encompasses. Potvin et al. (2020) identified as many as 86 different conceptual change models that are available in science education as interpretations and further developments of the basic model.

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enter the classroom without any conceptions of the subject matter that will be taught and in the classroom accumulate knowledge from scratch. Instead, the model assumes that students enter into learning situations with their own collections of (pre-)conceptions about the subject matter and build new knowledge starting from these initial conceptions. The model thus acknowledges that before engaging in instruction, students will have acquired a range of conceptions about scientific topics from a variety of sources, including their earlier education, their parents, their peers, movies and shows, articles on the internet, social media, books, and so on. These conceptions inevitably constitute a starting point for their further learning: "students must build new ideas in the context of old ones, hence the emphasis on "change" rather than on simple accumulation or (*tabula rasa*, or "blank slate") acquisition" (DiSessa, 2014: 88).

Some such initial conceptions may be wholly mistaken, others may miss the mark by larger or smaller degrees, and still others may already correspond well to currently accepted scientific concepts and thus do not need to be changed much. Accordingly, the task for educators is to provide a learning context in which students can relate their own conceptions to those concepts that are accepted in the various sciences, identify discrepancies between these two sets of concepts, and transform those initial conceptions that need correction (usually called "misconceptions", or sometimes "alternative conceptions") into an understanding of concepts that are as close as possible to the accepted scientific concepts. As Cunningham and Wescott (2009: 505), for example, put it:

> *"College students do not come to biological sciences classes [...] as "blank slates." Rather, these students have complex and strongly held scientific misconceptions that often interfere with their ability to understand accurate explanations that are presented in class. Research indicates that a scientific misconception cannot be corrected by simply presenting accurate information; the misconception must be made explicit, and the student must decide for him or herself that it is inaccurate."*

The general model thus crucially rests on a contrast between a student's conceptions and the concepts that are currently accepted in the sciences, and sees teaching as a movement from the former to the latter. Anderson et al. (2002: 953), for example, write: "Alternative conceptions are ideas that differ from the corresponding scientific explanations. [... T]hese alternative ideas can serve as anchoring conceptions [...] from which to move to a scientific conception when suitable instructional strategies are developed."

Much research in science education on conceptual change has focused on the starting point of this movement from misconceptions to correct concepts by extensively mapping out the variety of initial conceptions that are present with students at various educational levels and regarding a variety of topics in the natural and life sciences, teachers' awareness of these initial conceptions, and potential tools available to teachers to address them. To some extent, this research also addressed the end point of the movement by relating widespread initial conceptions to currently accepted scientific concepts as well as to concepts that were entertained at some point in the history of a particular area of science but were later displaced. An example of such research is the extensive work done by researchers in science education (on some occasions collaborating with historians and philosophers of biology) on students' initial conceptions of central concepts in evolutionary biology, such as 'species', 'inheritance', 'selection', 'fitness', 'common descent', and so on.[2] This research has resulted in a clear picture of how students' conceptions match – or fail to match – current technical concepts in evolutionary biology and how they sometimes match displaced, older technical concepts (and thus connect to past stages of evolutionary thinking but miss the current stage), providing educators with a "roadmap" for teaching evolution.

In addition, in the field of science education this research has led to extensive criticism of the general model of conceptual change and prompted several further developments, such as the "knowledge in pieces" approach (DiSessa, 2002, 2014, 2018; DiSessa & Sherin, 1998), the "guided reinvention" approach (Geraedts & Boersma, 2006), the "framework theory" approach (Vosniadou, 2019), and the "dynamic model of conceptual change" (Nadelson et al., 2018).[3] One prominent criticism is that processes of conceptual change are much more complex and diverse than the general model acknowledges and, in particular, do not consist in the straightforward replacement of initial concepts by more adequate ones. DiSessa, for example, argued that "much prior research in conceptual change has taken a vastly oversimplified view of the process" (DiSessa, 2002: 29) by, among other things, assuming an oversimplified view of the nature of concepts that fails to acknowledge the diversity of units of mental content involved in conceptual change processes as well as their complex interconnections, and a lack of detailed explications of how processes of conceptual chance actually take place in practice. Instead, DiSessa advocates a "conceptual ecology" approach that closely examines how concepts and other units of mental content are used in the particular environments in which they feature and how they change in these environments. Such an approach would involve a "move toward a systems view that describes scientific concepts as complex, finely configured systems involving named parts and relations" (DiSessa, 2002: 58). This approach treats concepts not as simple units of mental content where existing units are replaced by new ones as a person learns, but as complex and fluid systems that gradually change as parts are

[2] This research has yielded a very large body of literature. Examples include: Brumby (1979; 1984), Lawson & Thompson (1988), Bishop & Anderson (1990), Green (1990), Jiménez-Aleixandre (1992; 1994), Settlage (1994), Demastes et al. (1995), Abimbola & Baba (1996), McComas (1997), Ferrari & Chi (1998), Anderson et al. (2002), Fisher & Moody (2002), Geraedts & Boersma (2006), Kampourakis & Zogza (2007; 2009), Nehm & Reilly (2007), Nehm & Schonfeld (2008), Abraham et al. (2009), Baumgartner & Duncan (2009), Burton & Dobson (2009), Cunningham & Wescott (2009), Gregory (2009), Bean et al. (2010), Pazza et al. (2010), Nehm et al. (2010; 2012), Van Dijk & Reydon (2010), Andrews et al. (2011), Furtak (2012), Linnenbrink-Garcia et al. (2012), Keskin & Köse (2015), Stern et al. (2018), Kampourakis (2020a; 2020b).

[3] I only mention these four approaches to acknowledge the work done by researchers in science education in response to the problems the general conceptual change model faces. As these approaches do not play a role in my argumentation, I will not discuss them here. For some criticisms of the model from the side of researchers in science education, see, e.g., DiSessa (2002), Limón & Mason (2002), Mercer (2008), Treagust & Duit (2008).

removed, added or replaces, and connections between parts are installed, removed, weakened, or strengthened.[4]

An important aspect of these criticisms and developments is the rejection of a central assumption in some versions of the conceptual change model. This is the assumption that there is a clear aim for every instance of conceptual change, namely the correct, accepted technical concept or set of concepts as it features in our best current science. That is, the model assumes that students should "learn the concepts that are *the targets of instruction*" (Carey, 2000: 13; emphasis added). In contrast to this assumption, criticisms such as DiSessa's show that there are no clear-cut conceptual targets of instruction, but that the targets rather are complex networks of various knowledge elements.

In this paper, I aim to achieve three things. First, I want to show how contemporary work in the history and philosophy of science on conceptual pluralism supports the rejection by researchers in science education of the assumption of clear-cut conceptual targets for instruction. Such targets, I suggest, are lacking in many cases. Second, I want to show how history and philosophy of science provides tools to deal with this lack of clear conceptual targets of instruction in educational practice. Rather than providing a general argument in support of general conclusions, I will argue by example and examine one prominent case of conceptual pluralism in biology, namely the concept of fitness (and I will briefly also consider a closely related concept, namely the concept of natural selection). Based on a brief discussion of the philosophical debate, I suggest a conceptual toolkit that can be used to connect misconceptions and scientific conceptions of fitness in teaching contexts in secondary education and tertiary education. The contexts I have in mind are those in which the topics of evolution, natural selection and fitness are explicit parts of the subject matter, such as advanced-level biology classes in secondary education, undergraduate and graduate biology classes in universities as well as biology teacher training programs. This examination of the case of fitness also serves to achieve my third aim, namely to show how history and philosophy of science can make important contributions to both the theory and practice of science education.

This paper thus is intended as a contribution at a practical level to science education in the area of evolutionary science and (at a metalevel) as a contribution to the reflection on the relation between science education and history and philosophy of science that shows how results from history and philosophy of science can inform science education. The case of fitness constitutes a clear example in which history and philosophy of science offers tools for teaching that can be employed in teaching scientific content to science students as well as in training future science teachers. These tools do not only make science teaching more adequate to the actual state of affairs in the sciences, but at the same time bring a core element of work in history and philosophy of science (the detailed analysis of scientific concepts, and their historical development and diversification) into the science classroom.

[4] For more details on this approach, see DiSessa & Sherin (1998) and DiSessa (2014; 2018).

2 Fitness and selection: misconceptions and philosophy

In the past four decades a large volume of literature in science education has accumulated on students' misconceptions about evolution and central concepts in evolutionary theory, as well as tools for addressing them (see Footnote 2 above). A general finding from these studies is that such misconceptions are not only widespread among younger children, but also among high school students, university students not majoring in biology, and even university-level undergraduate biology majors. These misconceptions often are strongly resistant to change (Anderson et al., 2002: 953; Fisher & Moody, 2002: 56) and, in particular for terms that commonly occur in everyday language but also have very technical scientific meanings can constitute obstacles to the acquisition of technical scientific concepts (Cunningham & Wescott, 2009: 506; Nehm et al., 2010: 605–606). 'Fitness' and 'selection' are prominent examples of the latter kinds of terms.

Detailed research has shown students to encounter a variety of problems when learning about evolution by natural selection and to possess a variety of misconceptions relating the concept of selection and associated concepts.[5] Widespread misconceptions pertain to the origins of mutations (where mutations are often seen as induced rather than spontaneously occurring), the failure to appreciate the probabilistic nature of Darwinian evolution, views of adaptive change as guided by the needs of organisms to survive, the failure to distinguish between the development of organisms and the evolution of populations (the view that individual organisms adapt rather than seeing that adaptation is a population-level process), anthropomorphic conceptions of selection as performed by a selecting agent, and more. As many misconceptions are related to the concept of fitness, I will focus on that concept in what follows.

With respect to the concept of fitness, several widespread misconceptions have been identified. These include (but are not limited to):

(1) Views that 'fitness' means physical strength (Abraham et al., 2009; Bishop & Anderson, 1990) or other organismal traits that are beneficial in competitive environments, such as health, speed, intelligence, agility, etc. (Anderson et al., 2002; Demastes et al. 1995; Keskin & Köse, 2015; Nehm & Schonfeld, 2008);
(2) The view that natural selection causes *only* the very fittest organisms to survive (Keskin & Köse, 2015);
(3) The view that individual organisms can change to better fit into their environments (Demastes et al. 1995; Ferrari & Chi, 1998; Furtak, 2012; Geraedts & Boersma, 2006; Keskin & Köse, 2015; Linnenbrink-Garcia et al., 2012);

[5] See Brumby (1979; 1984), Lawson & Thompson (1988), McComas (1997), Anderson et al. (2002), Geraedts & Boersma (2006), Nehm & Reilly (2007), Nehm & Schonfeld (2008), Gregory (2009), Nehm et al. (2010; 2012), Van Dijk & Reydon (2010), Andrews et al. (2011), Keskin & Köse (2015), Stern et al. (2018) and Kampourakis (2020a; 2020b).

(4) The view that fitness is a property of species rather than organisms, in the sense that the fittest species prevail (Nehm & Reilly, 2007; Nehm & Schonfeld, 2008);
(5) The view that the term 'fitness' applied to genes means that an allele is dominant, as opposed to recessive (Nehm & Reilly, 2007; Nehm & Schonfeld, 2008).

Misconception (1) clearly corresponds to everyday meanings of the words 'fit' and 'fitness' associated with physical exercise and overall health. Misconception (2) reflects Herbert Spencer's phrase "survival of the fittest", which – even though it originated in the scientific literature – has become so commonly known as a shorthand for evolution by natural selection that it can now be seen as part of everyday language.[6] Misconception (3) is often interpreted as a Lamarckian conception of evolution and taken as an indication that students enter the classroom with a Lamarckian perspective on evolution that must be transformed into a Darwinian perspective.[7] As Crow (2004: 64) put it, "Lamarck is sitting in the front row". Misconceptions (4) and (5) are less rooted in everyday views of evolution and may represent inadequate understandings of scientific content that was acquired by students in earlier instructional contexts.

Starting from such inventories of misconceptions, adherents of the conceptual change model (including active teachers) sometimes see the challenge as consisting in finding ways to transform these misconceptions into *the* correct biological concept of fitness. The same view is held for closely related notions such as 'selection'. Furtak (2012), for example, mentions teachers who in interviews expressed the view that misconceptions needed to be "debunked" or "squashed", and aligns with the view that "students are likely to confuse everyday meanings of "fitness" with *the biological definition of the term*" (2012: 1189; emphasis added). Similarly, Ferrari & Chi claim that "the notion of natural selection is remarkably simple" (1998: 1231) and speak of students having naïve views of the mechanism of natural selection, suggesting that there is an unequivocal scientific view that teaching should aim for. But philosophical work on the notions of natural selection and fitness show that conceptual change is much less simple than these authors think.

Among historians and philosophers of biology there is an ongoing debate on the question what, exactly, natural selection *is*: a force, a process, a mechanism,[8] or rather just the statistical *outcome* of other natural causes, processes or mechanisms.[9] Matthen & Ariew, for example, argue that "[f]itness and natural selection have no reality except as accumulations of more fundamental events" (2002: 82) – a view which yields completely different concepts of fitness and natural selection than are usually taught in biology classes and textbooks. History and philosophy of science thus show us that the of natural selection is not a simple notion at all, *contra* Ferrari

[6] The phrase was coined by Spencer and suggested to Darwin by Alfred Russel Wallace, who thought it expressed Darwin's ideas more clearly than the phrase "natural selection". Darwin incorporated it in the fifth and sixth editions of the *Origin of Species*.

[7] See, for example, Jiménez-Aleixandre (1992), Demastes et al. (1995) and Fisher & Moody (2002). Geraedts & Boersma (2006) and Kampourakis & Zogza (2007) argue that this interpretation is incorrect.

[8] E.g., Sober (1984), Skipper & Millstein (2005), Garson (2013) and Millstein (2013).

[9] E.g., Matthen & Ariew (2002; 2009), Walsh et al. (2002; 2017), Lewens (2010), Huneman (2012).

and Chi (1998), and that there is a plurality of possible conceptual targets of instruction in the teaching of evolution. Largely independently of this metaphysical debate on the nature of natural selection, there is a similar debate on the concept of fitness. This extensive debate, which has a history of more than five decades and is still very far from resolved, is carried out by historians and philosophers of biology as well as biologists themselves.[10] The latest major event in this debate is a heated controversy following a criticism of the concept of inclusive fitness (Allen & Nowak, 2016; Allen et al. 2013; Nowak et al., 2010). The criticism was noteworthy because one of its authors (E.O. Wilson) long was a major proponent of inclusive fitness theory who had apparently revised his views (Woodford, 2019). It led to a highly critical response authored by 137 biologists (Abbott et al., 2011) and the publication of special criticism-and-response sections and special issues devoted to the controversy, and started a still unresolved discussion among biologists and philosophers of biology.[11]

These debates show one thing particularly clearly: neither for the concept of natural selection nor for the concept of fitness clear target concepts in biological science exist. For the concept of fitness, there isn't even clarity regarding the number of different fitness concepts, their relations to each other, or their usefulness in biological research. Note that the concept of fitness is not special in this respect, but rather an instance of a common state of affairs in the sciences. Historians and philosophers of science (and in particular of biology) have come to endorse pluralism regarding many central scientific concepts – in biology for instance with respect to the concepts of species, gene, function, fitness, individual, and others (see, prominently, Dupré, 1993). Indeed, "[i]t is only a slight exaggeration to say that conceptual pluralism is taking over debates in (philosophy of) science" (Taylor & Vickers, 2017: 17). Conceptual pluralism as a stance in the history and philosophy of science amounts to acknowledging that it cannot be generally expected that there are uniquely correct meanings for central concepts in the sciences. Technical scientific terms often have related but different meanings in different contexts of scientific research and it is not uncommon for different meanings to be used in parallel to serve different purposes in different contexts of research (Taylor & Vickers, 2017: 17–18; Kampourakis, 2018). In addition, for many concepts there are ongoing, open-ended debates about their meanings, with participants in the debates finding themselves unable to find clear ways to adjudicate between competing interpretations.

[10] The literature generated in the debate on fitness concepts is vast and impossible to review here (but for an overview of the main aspects, see Sect. 3.1). Good introductions to the literature are Hendry et al. (2018) and Rosenberg & Bouchard (2020). Work by philosophers of biology includes Manier (1969), Beatty & Mills (1979), Matthen & Ariew (2002), Ariew & Lewontin (2004), Bouchard & Rosenberg (2004), Krimbas (2004), Ariew & Ernst (2009), Van Dijk & Reydon (2010), Abrams (2012), Birch (2017), Rubin (2018) and Bruner & Rubin (2020). Work by biologists includes De Jong (1994), Wilson (2004), Demetrius & Ziehe (2007), Orr (2009), Akçay & Van Cleve (2016) and Hendry et al. (2018).

[11] E.g., Rousset & Lion (2011), Birch (2017), Rubin (2018) and Levin & Grafen (2019). See also a *Brief Communications Arising* section in *Nature* 471 (2011): E1-E10, a special collection of *Royal Society Open Science* (https://royalsocietypublishing.org/topic/special-collections/inclusive-fitness), and a dedicated website by the critics whose publications started the controversy (https://ped.fas.harvard.edu/inclusive-fitness).

Conceptual pluralism deeply complicates the teaching of scientific concepts to students on the conceptual change model, as the "targets of instruction" often are not unequivocally and clearly defined scientific terms, but complicated manifolds of concepts and technical terms associated with a plurality of meanings. The general lesson to draw from this literature is that there are no clear targets for conceptual change. The "target of instruction" is often not an unequivocally and clearly defined scientific term, but rather a complicated bundle of concepts and terms that are subject to ongoing debate, modification and revision. The target of instruction thus is a diffuse, moving target, such that teaching *the right concept* of fitness (*the* textbook definition of 'fitness'), or *even the right set of concepts*, cannot be an aim of science teaching. This constitutes a problem for views that conceptual change means bringing the diversity of students' initial (mis-) conceptions as close as possible to the scientifically accepted target concepts. But I want to suggest that philosophy of science provides tools to address this problem, and I now turn to exploring these tools and will illustrate them by focusing on the notion of fitness.

3 Using philosophy to teach non-philosophers

Conceptual clarification – one of the core tasks in the history and philosophy of science – can yield tools to address students' alleged misconceptions more adequately than is done in the conceptual change model and to see the hidden value that misconceptions may have even if strictly speaking they are wrong.[12] Notwithstanding the complicated nature of the debate on the notion of fitness, the philosophical literature highlights several meanings of the term that played leading roles at some point in the history of biology. Noteworthy about these meanings is their closeness to widespread misconceptions, allowing them to be used to address these in the classroom. For reasons of space, I will only be able to give an incomplete overview of the conceptual clarification of the concept of fitness that philosophers of biology have undertaken. Note, too, that as research in history and philosophy of biology progresses, new meanings may be uncovered, such that any overview of the different meanings of 'fitness' will inherently be provisional and incomplete.

3.1 An incomplete conceptual clarification of 'fitness'

The first meaning of 'fitness' – *Darwinian fitness* (Ariew & Lewontin, 2004: 348–350) or *ecological fitness* (Rosenberg, 2006: 165–169) – is that of an organism's fitness as a metaphorical "lock-and-key" fitting into its environment (Krimbas, 2004: 186). This notion of fitness served an explanatory role in Darwin's theory of natural selection: organisms that match the demands placed on them by their environments better than others (i.e., have traits that meet their needs in their particular environment) clearly have

[12] Therefore, it might be better to stop referring to students' initial conceptions as 'misconceptions' but instead use a more value-neutral term such 'initial conceptions' or 'alternative conceptions' (Van Dijk & Reydon, 2010: 656).

a better chance of survival and reproduction than their less well matching compatriots. As Ariew and Lewontin (2004: 348) write, "[d]ifferent individual members of a species […] 'fit' into the environment to different degrees as a consequence of their variant natural properties, and those that made the best 'fit' would survive and reproduce their kind better than those whose 'fit' was poorer." This formulation clearly shows that Darwinian fitness can be attributed to individual organisms (Krimbas, 2004: 186) – no two organisms will have exactly the same Darwinian 'fit' with their environment, as no two organisms will be identical in each and every trait. But note that nothing prevents us from attributing Darwinian fitness to types of organisms, i.e., phenotypes, rather than individual organisms. Darwinian fitness compares actual organisms with respect to their 'fit' with their environment, but it is also possible to take abstract phenotypes (types of organisms defined by the same trait or traits) and compare these with respect to their 'fit' into the environment. The comparison is the same, but in one case actual organisms are compared while in the other case abstract types are compared. While Darwinian fitness is not commonly attributed to phenotypes, it is a possible fitness concept that should be distinguished from the classical concept of Darwinian fitness as two variants of the same concept. Here, I will distinguish between 'Darwinian fitness [organism version]' and 'Darwinian fitness [type version]'.

Because of several problems with the concept(s) of Darwinian fitness (Rosenberg, 2006: 165–166) and with the rise of population genetics, biologists increasingly replaced this notion by a notion of fitness as the *actual reproductive success* of organisms, meaning the number of actual offspring that survive to reproductive age.[13] This move involves a fundamental shift from conceptualizing fitness in terms of what explained differential reproduction to conceptualizing fitness in terms of differential reproduction itself. That is, while the notion of 'Darwinian fitness' is conceived in terms of the properties of organisms that give them a particular reproductive success, on this new concept fitness is conceptualized as reproductive success itself (i.e., the *explanandum* of Darwinian fitness). This fitness concept, which I will call 'individual actual fitness', can be thought of as an absolute or relative value: "absolute fitness is the fitness of a biological unit (e.g., number of offspring of an individual) ignoring the fitness of other units (e.g., other individuals in the population), whereas relative fitness is the fitness of a unit relative to those other units (e.g., number of offspring of an individual divided by the mean number of offspring per individual in the population)" (Hendry et al., 2018: 460). Note that in principle, actual fitness can be attributed to various concrete biological entities, such as organisms, genes and groups, but not to types. Types, after all, do not have any actual (non-averaged) reproductive success, only concrete biological entities do.

This concept of fitness was soon found problematic too, though, because the life history of organisms is affected by chance events and accidents not related to their traits and that therefore cannot count as explanatory factors in evolutionary theory (Krimbas, 2004: 186; Van Dijk & Reydon, 2010: 667). A way to avoid this problem is to attribute fitness to organism types rather than individual organisms, and conceive of fitness as the *average actual reproductive success of organisms*

[13] See Ariew & Lewontin (2004: 350ff.), Van Dijk & Reydon (2010: 667) and Akçay & Van Cleve (2016: 2).

of a particular type. This conception, which I call 'average actual fitness', attributes identical fitness to organisms of the same type (in the same way as Darwinian fitness [type version] does), connecting fitness to the intrinsic traits shared by all organisms of a type and bracketing effects of chance events on actual individual reproductive success. A problem with this conception, however, is that fitness still is equal to actual reproductive success, thus merely referring to the phenomenon in need of an explanation rather than to an evolutionary explanation of this phenomenon (Van Dijk & Reydon, 2010: 668). In addition, biology emphasizes variation among the organisms of a population or species, rather than sameness of organisms of a type, such that a concept of average actual fitness of a type does not seem to do much explanatory work in biological science. Beatty and Mills (1979) avoided this by *defining* organism types in terms of shared traits (Van Dijk & Reydon, 2010: 669), such that organism types are abstractions and no two actual organisms will be of exactly the same phenotype, as they will never have perfectly identical physical strength, speed, agility, etc. When considering phenotypes this may not yield a very useful fitness concept, but on a view of organism types as genotypes organisms *can* have identical genetic traits (i.e., alleles), such that for genotypes such a fitness concept could be more useful there.

In response to the problems confronting notions of individual actual fitness and average actual fitness, Beatty and Mills (1979) proposed to conceive of fitness as the capacity of organisms with a particular set of phenotypic or genotypic traits (i.e., a type of organism) to have a particular degree of reproductive success in a given environment. This is the famous *propensity interpretation of fitness*, which in the same way as Darwinian fitness is intended to serve as an explanation of actual reproductive success rather than as a term denoting the explanandum. Because the concept of fitness (in the same way as other scientific terms) should perform an explanatory role, conceptualizations that refer to an explanans are to be preferred over conceptualizations that merely refer to an explanandum. In contrast to the concepts of individual and average actual fitness, on the propensity interpretation fitness refers to the capacity or propensity of biological entities of a particular type to produce offspring. One thing to note is that on this interpretation a given organism has a fitness only as an instantiation of a particular type – fitness thus is attributed to types and only indirectly to organisms and other biological entities as the "expected fitness of a unit given its genotype or phenotype" (Hendry et al., 2018: 460). This way of conceptualizing fitness has become prominent in biological research. Unfortunately and confusingly, it is often called 'Darwinian fitness'. Demetrius and Ziehe, for example, write that "[t]he term Darwinian fitness refers to the *capacity of a variant type* to invade and displace the resident population in competition for available resources. […] Fitness, according to Darwin, means the capacity to survive and reproduce." (Demetrius & Ziehe, 2007: 323; emphasis added). In a similar vein, Dietz (2005: 1097) specifies that "Darwinian fitness [is] the capacity of a rare mutant to prevail in competition with the ancestral type." To distinguish this fitness concept from Darwinian fitness as discussed earlier in this section, I will here use the term 'propensity interpretation'.

Somewhat separated from these conceptual developments, the concept of *inclusive fitness* was proposed by Hamilton in the 1960s.[14] Hamilton pointed out that organisms can contribute their genes to their offspring population either directly (by producing offspring themselves) or indirectly (by helping relatives that have similar genotypes to ensure the survival of their offspring). 'Inclusive fitness' can be thought of as the actual number of offspring caused directly or indirectly by an organism (Rubin, 2018), or the "weighted sum of the effects on reproductive success it causes by means of its behaviour [where t]he weights are coefficients of relatedness" (Birch, 2017: 2). The concept thus counts an organism's own offspring as well as offspring of relatives to the survival of which the organism contributed indirectly, where offspring of more distant relatives is given less weight in the total count. This fitness concept is similar to that of individual actual fitness, as fitnesses are attributed to individual organisms based on their actual reproductive success (with the difference that now indirect offspring in later generations is counted too). The concept was intended as an explanation of the evolution of social behavior in the context of kin selection theory, but (as mentioned in Sect. 2) its usefulness has become the topic of recent debate.

3.2 From conceptual clarification to a toolkit for teaching

The conceptual clarification presented above is incomplete, as it presents only the main results from research in the history and philosophy of biology on the notion of fitness. The volume of literature on the topic is extensive and for reasons of space, more details cannot be given here. But the preceding overview suffices to develop a conceptual toolkit for teaching. Before continuing, though, I should caution readers that the notion of a conceptual toolkit is not intended as a very strict notion, nor as a notion that has deep theoretical roots in previous research. I use the term 'conceptual toolkit' in an informal sense to denote *a set of concepts and conceptions available to students, teachers and researchers to work with in their learning, teaching and research practices*. The various concepts and conceptions in the toolbox in this informal sense are tools for epistemic and didactic work: cognitive agents use concepts to organize their knowledge and understanding of the world as well as their activities of the production of knowledge and understanding.[15] The conceptual toolkit regarding the concept of fitness developed here thus is just a set of concepts and conceptions that can be used by students and teachers in teaching practice.

[14] See Mills & Beatty (1979: 285), Van Dijk & Reydon (2010), Akçay & Van Cleve (2016), Rubin (2018), Levin & Grafen (2019) and Bruner & Rubin (2020).

[15] In science education, Taber (1995) presented the notion of a mental toolbox containing concepts as an analogy for discussing learning processes. Philosophers of science also sometimes refer to concepts as parts of conceptual toolkits: Odenbaugh & Griffiths (2020), for example, write that "[t]he idea of *proper function* has become part of the conceptual toolkit of philosophy in general and of the philosophy of language and the philosophy of mind in particular […]." For more on the idea of concepts as tools for research with specific roles in specific contexts, see e.g., Stotz & Griffiths (2008), Stotz (2009) or Brigandt (2010).

The conceptual clarification that was presented above shows several aspects of the concept of fitness. First, it shows that instead of one fitness concept, at least four distinct concepts should be distinguished – Darwinian (or ecological) fitness, individual actual fitness, average actual fitness, and inclusive fitness. In addition to these different meanings of 'fitness', it became clear that there are different views in the literature regarding which entities can be bearers of fitness. Fitness can be attributed to genes, organisms and organism types (which can be defined as phenotypes or genotypes) (see also De Jong, 1994: 4). Sometimes, they even can be attributed to populations, lineages and species (Orr: 2009: 531).[16] Accordingly, two dimensions of fitness can be distinguished: the *content* of fitness as an attribute and the *entity* to which this is attributed.

It is thus possible to develop a simple framework onto which different meanings of 'fitness' can be mapped[17]:

'Fitness' can mean

a. *a degree of matching between traits and environment;*
b. *actual reproductive success (absolute, relative, or average number of direct offspring);*
c. *a propensity for reproduction;*
d. *inclusive reproductive success (number of offspring to which a contribution was made)*

of

i. *an individual organism;*
ii. *a phenotype (a type of organism);*
iii. *a gene;*
iv. *a genotype (a type of organism);*
v. *a population;*
vi. *a lineage or species.*

Figure 1 graphically represents the framework as a 4×6 matrix. Each slot represents a specific conception of fitness (a particular meaning of 'fitness' combined with the entity or type to which fitness is attributed). The matrix is what I call a 'conceptual toolkit': it is a set of conceptions associated with the concept of fitness that can be used in research, teaching and learning practices. Note that not all slots necessarily constitute possible or useful conceptions, such that not all slots are necessarily filled. For example, concepts of the inclusive fitness of organisms types are not possible, because inclusive fitness encompasses the *actual* contribution of an

[16] For reasons of space, I have not considered this point in any detail. Suffice it to say that on interpretations of evolution that include group selection or species selection, fitness can be attributes to populations (groups), species, and/or lineages as these entities produce different numbers of descendant entities.
[17] For a different framework, see Abrams (2012).

'Fitness'	***a.*** **degree of matching**	***b.*** **actual reproduction**	***c.*** **propensity for reproduction**	***d.*** **inclusive reproduction**
i. **organism**	*Darwinian fitness* [organism version]; *Ecological fitness* [organism version]	*Individual actual fitness*	(Possible fitness concept only in a derived sense)	*Inclusive fitness*
ii. **phenotype**	*Darwinian fitness* [type version]; *Ecological fitness* [type version]	*Average actual fitness*	*Propensity interpretation*	
iii. **gene**		*Individual actual fitness*	(Possible fitness concept only in a derived sense)	
iv. **genotype**		*Average actual fitness*	*Propensity interpretation*	
v. **population**		*Individual actual fitness*		(Unclear)
vi. **lineage, species**		*Individual actual fitness*		(Unclear)

Fig. 1 The framework depicted as a 4×6 matrix with some examples of what the slots can contain. For each slot, is can be asked whether it would contain a meaningful and useful concept of fitness for biological science, or for everyday understanding of and communication about evolution. Some slots remain empty, as not all fitness concepts can meaningfully be attributed to all six kinds of biological entities in the table. The concepts in slots *c.i.* and *c.iii.* are derivative on those in slots *c.ii.* and *c.iv.*, respectively. Note: slots filled in light grey do not contain a possible fitness concept

organism to the production of offspring. Note too, again, that this is a simplified and incomplete toolkit, derived from an abbreviated conceptual clarification and not intended as an exhaustive description of all the different meanings of 'fitness' that can be found in biological science. More detail can be added on the basis of a closer examination of the literature and of the history and contemporary practice of biological research. That is, I do not claim that the toolkit presents all there would be to say about the concept of fitness – far from it, it is a starting point for further work.

Regarding the content of the slots, I want to suggest that this can consist of concepts as well as conceptions. Some authors (e.g., Carey, 2000, quoted in Sect. 1) take concepts, not conceptions, to be the targets of instruction. Strictly speaking this is incorrect, as often a clear distinction is made between conceptions and concepts. According to Kampourakis (2020a: 42), for example, "[c]oncepts should be distinguished from conceptions, the latter being the different meanings of, or meanings associated with, particular concepts." On such a view, scientific concepts are technical terms, such as 'species' or 'temperature', for which textbooks provide definitions, and conceptions are the various meanings of this concept that exist in the minds of cognitive agents. The textbook definitions of scientific concepts then provide widely accepted meanings of the term (strictly speaking, definitions are verbalizations of scientific *conceptions*), while each cognitive agent has its own conception associated with the term. (Even someone who memorizes a textbook definition of 'species' will have their own personal conception associated with the concept of species, because the definition will be placed in the context of that person's own knowledge, beliefs and experiences.) The movement from misconceptions to correct concepts (see Sect. 1) thus strictly speaking is from a person's initial conception associated with a concept to one of the available scientific conceptions of that concept. But there is a debate in psychology, and in the philosophy of mind and language, on the nature of concepts and on how conceptions relate to concepts (e.g., Ezcurdia, 1998; Margolis & Laurence, 2019). In those fields, concepts themselves are often understood as units of mental content that can be thought of as mental representations in the minds of cognitive agents, abilities of cognitive agents, or abstract objects. On the former two views of the nature of concepts, there is no difference between concepts and conceptions: both are units of mental content exiting in the minds of cognitive agents. Because of the lack of clarity on the nature of concepts and on the distinction between concepts and conceptions (and because such a distinction is not important for my arguments in the present paper), I will ignore this issue and not make a strict distinction between concepts and conceptions.

Let me now illustrate the conceptual toolkit in more detail. I want to suggest that its function is to map out the various concepts and conceptions in such a way that for each concept/conception it shows how fitness is conceived of ontologically – as a physical property or set of properties; as a measure of actual or average reproductive success; as a capacity or propensity – and to what kind of entities it is attributed. As concepts can be thought of as tools for research, for communication, for understanding, and so on (see Footnote 15), Fig. 1 can be thought of as depicting part of the toolkit available to researchers, teachers and students with respect to the scientific term 'fitness'. In teaching contexts, the toolkit can be used by instructors as well as students to locate currently used scientific concepts they encounter in the literature, concepts found in older texts (that were used at an earlier stage of the history of biology but now might have become obsolete), widespread alternative/everyday conceptions and individuals' own conceptions in relation to each other.

Consider for instance Demetrius and Ziehe's (2007) research article, which might feature in a university-level course in population dynamics. The authors use 'Darwinian fitness' to mean "the *capacity* of a variant *type* to invade and displace the resident population in competition for available resources" (Demetrius & Ziehe: 2007: 232; emphasis added). In the toolkit, this conception would be located in slot *c.ii.* or *c.iv.*, whereas Darwinian fitness in the traditional sense discussed further above is located in slot *a.1.* The toolkit thus helps to clarify that the term as used by Demetrius and Ziehe (2007) is an instance of the propensity interpretation of fitness and as such is very different from the same term as used by Ariew and Lewontin (2004).

The same can be done for students' alternative conceptions. While misconception (1), mentioned above, strictly speaking is incorrect, it still connects in important ways to Darwin's conception. While Darwin did not use the term 'fitness' explicitly, he did have an implicit concept and "took it to capture a property of an individual, viz., a physical property of the organism accommodating to its way of living, and thus a cause which explains the success of individuals subjected to the process of natural selection" (Krimbas, 2004: 186). Although this concept is no longer used in biological research, it is of immense historical importance when it comes to understanding the fundamental idea of evolution by means of natural selection. It is a very important part of the conceptual toolkit for the teaching of evolution and is found in slots *a.i.* and *a.ii.* By examining column *a* in more detail, teachers can address various aspects of the concept of Darwinian fitness. One such aspect is the fact that there must be two different versions of the same concept, because attributing physical properties to individual organisms and comparing their fitness is different from defining organism types by physical properties and comparing the fitness of types. While the concept in slot *a.i.* is useful for comparing actual organisms in a population (with respect to the question why one reproduced better than another), the concept in slot *a.ii.* is useful for comparing traits (with respect to questions which trait will give organisms a general advantage over their competitors). Another such aspect is the fact that when fitness is conceptualized in terms of physical properties, fitness can only be attributed to entities that possess physical properties that affect their reproductive success. Asking students why slots *a.iii.–a.vi.* are empty can bring this aspect into focus and yield a better understanding of the concept of Darwinian fitness.[18]

Furthermore, when discussing Darwinian fitness it must be emphasized that Darwinian fitness is a *relational* property – as an organism with a good "lock-and-key" fit for one environment may fit other environments very badly – rather than a property of an organism considered by itself (Van Dijk & Reydon, 2010: 667). But this aspect of the concept does not diminish the importance of the organism's properties. Thus, a classroom discussion can address misconception (1) by identifying its specific target (conceptions in slot *a.1.*), identifying a scientific concept connected to that target (Darwinian fitness), and subsequently showing how misconception (1) is partly inconsistent – but also partly consistent – with the concept of Darwinian fitness. This allows the discussion to highlight the scientific value contained in misconception (1), even though taken literally it is incorrect, rather than simply presenting it as a wrong conception. The same can be done with misconception (3), which also connects to slot *a.1.*, and misconception (4), which connects to all slots in dimensions *v.* and *vi.*

The toolkit can also give classroom discussions more depth by highlighting the *extent* of the conceptual diversity relating to the term 'fitness' (by graphically showing a 4×6 matrix of potential concepts) and the *reason* for this diversity. This reason is clearly seen in the philosophical debate on the concept: authors assess the various conceptions of fitness for their *usefulness* for various tasks in biological research and explanation. De Jong (1994: 3), for example points out that classical Darwinian fitness "seems unproductive in evolutionary biology"

[18] Genes, populations and lineages/species can also be thought of as having physical properties that affect the number of their descendants. However, Darwin's concept predates accounts of gene selection, group selection and species selection, and in the context of these later accounts no matching fitness concepts were developed. Thus, versions of the Darwinian fitness concept in principle are possible for slots *a.iii.–a.vi.*, and discussion in educational contexts could focus on the questions why such versions are not prominent parts of current biological science and whether they could play important roles in biological research.

and Ariew and Lewontin (2004: 347) emphasize that Darwinian fitness and actual reproductive fitness "are distinct concepts coming from distinct explanatory schemes." Krimbas (2004) similarly discussed several concepts and variants of concepts, including Darwin's concept, Malthusian fitness, Fisherian fitness and Wrightian fitness, with respect to what those concepts were intended to do and how well they performed on their specific tasks.[19] And the criticism of the concept of inclusive fitness by Nowak and co-authors, as well as the responses to these criticisms, hinge on the question whether inclusive fitness is a useful concept or not (Nowak et al., 2010: 1060; Abbott et al., 2011: E1).

Accordingly, each of the 24 slots can be examined with respect to the usefulness of their specific conceptions of fitness for biological research. Evolutionary theory provides the context for such an examination in the form of a description of the natural phenomenon that biologists study using the notion of fitness: differential reproduction due to different capabilities to survive and produce offspring in a particular environment. As Orr (2009: 531) put it:

> *"Although biologists have offered a staggering number of definitions of fitness, they agree broadly on the essence of the idea. In the crudest terms, fitness involves the ability of organisms — or, more rarely, of populations or species — to survive and reproduce in the environment in which they find themselves. The consequence of this survival and reproduction is that organisms contribute genes to the next generation."*

The natural phenomenon that is investigated using the term 'fitness' thus constitutes a unifying theme for the concept. It can be used to show why biology came to have a multitude of fitness concepts: biologists were (and still are) searching for good tools to study this natural phenomenon, and the various concepts associated with the term 'fitness' are such tools. The various concepts in the slots of the toolkit can thus be assessed with respect to their usefulness for their specific task in the investigation of this natural phenomenon. Conceiving of the term 'fitness' as referring to a conceptual toolkit and the debate as being about the usefulness of the various tools in the toolkit, I suggest, provides a more adequate picture of actual biological science than thinking of 'fitness' as a unified scientific concept.

Finally, using the toolkit to highlight the reason underlying conceptual pluralism regarding 'fitness' can also serve to show students two aspects of the "nature of science".[20] One is the fact that science often progresses by the multiplication of concepts, in which new concepts are introduced that completely shift the meaning of a term, rather than the clean replacement of old concepts by better ones. Such meaning shifts are represented in Fig. 1 by the four columns: moving between columns constitute movements between meanings. The history of the fitness debate is a history of introductions of new meanings and definitions next to earlier ones which were kept as

[19] Krimbas (2004: 188–189) also formulated criteria that any fitness concept would have to meet to perform a role in biological science.

[20] This is the topic of another extensive debate in science education. I cannot address it here, but see McComas (2020) for a recent state-of-the-art overview.

part of the biological vocabulary because to some extent they still served a scientific purpose. Relevant questions for the classroom with respect to old concepts then are, for example: What role did the concept play in the particular theoretical context in which it was used? Did that role become obsolete when its theoretical context was abandoned, or was the role (partly) carried over into the new theoretical context that we have today? If the old role was abandoned, why was it abandoned and was it abandoned for good reasons? Addressing such questions in the classroom will not only serve to provide students with a deeper understanding of the developmental history of their own field, but also can yield a deeper understanding of the concepts that are currently used in it. In this context, an exercise for students can be to try to allocate specific concepts found in philosophical and biological texts, such as the aforementioned concepts of Malthusian fitness, Fisherian fitness and Wrightian fitness, to one or more slots. When it comes to advanced concepts (Fisherian fitness, Wrightian fitness, inclusive fitness, etc.) such an exercise is probably more suitable for university-level undergraduate biology majors, such that the toolkit can be useful at various levels of secondary and tertiary education to bring results of work in the history and philosophy of biology into the science classroom.[21]

The second aspect of the "nature of science" is related to the first: the history of scientific concepts often is a history of intense debate, and conceptual pluralism is not a sign of deep confusion in an area of science but rather sign of good science. Consider the debate that followed the criticism of inclusive fitness theory by Nowak et al. (2010): not only is this a case of open debate among a considerable part of the relevant scientific community, it also is a case of an eminent member of the community (E.O. Wilson) changing his view on a particular part of scientific subject matter. Indeed, the history of fitness concepts is one long debate about the usefulness of various definitions, and the fitness debate can help to show how theoretical debates, changes of opinion and (occasionally heated) criticism are crucial elements of good science.

4 Conclusion and outlook

In this paper I have tried to show how introducing results from work in the philosophy of biology into educational contexts can improve the teaching of biological subject matter. I have used this work to add to criticisms of the conceptual change model, which plays an important role in science education, as not adequate to the actual state of affairs in evolutionary biology with respect to the technical term 'fitness'. The conceptual change model is too simple in that it assumes that the initial misconceptions of students should be replaced by the correct scientific concept(s) as it features in our currently best science. In the case of fitness, however, our best science encompasses an ongoing debate on what 'fitness' can

[21] The exercise described here has not yet been tried out empirically in teaching practice. Data regarding its efficacy in various teaching contexts are still lacking and accordingly I would encourage readers to try out the toolkit in their teaching to obtain relevant data.

and should mean, and does not provide us with *the* correct concept(s). Science teaching should adequately present this debate to students and I have attempted to show how results from the history and philosophy of science can be used to achieve more adequacy in this respect.

I have suggested a simple and incomplete conceptual toolkit that can be used to introduce the debate on ‘fitness’ and related scientific terms into the classroom in a well-ordered way. The toolkit is not intended as a complete and final representation of the debate on fitness concepts in the philosophy of biology, and as such is more a starting point for building more fine-grained conceptual toolkits than a ready-for-use item that can simply be taken off the shelf and applied in teaching contexts. I suggest that the toolkit can be used in teaching contexts as a first-order approach to fitness concepts that can be revised and further developed in the classroom as well as by students individually on the basis of discussions and further reading. Let me provide a brief outlook on what this could look like in practice.

First, the toolkit can metaphorically be compared to a provisional map that is amended as travelers discover more of the territory in which they travel. The 24 slots in Fig. 1 provide orientation into the philosophical and biological debate on fitness concepts, and this orientation can be improved as scientific conceptions are discussed, students bring alternative conceptions into the discussion (that may not fit into any of the 24 slots), and individuals read new literature that may include further conceptions. Working with the toolkit involves assessing where available scientific and alternative conceptions might fit into the 24 slots, asking what makes for a good fit and why a particular conception might or might not fit a particular slot, and adding slots if a need to do so is perceived. The foundation for asking this question is the usefulness of the conceptualization under scrutiny for research and for our general understanding of and communication about evolution. As scientific concepts are tools for research, for communication, for understanding, and so on (see above), asking whether a particular conceptualization fits (or should be made to fit) into the toolkit amounts to asking what work it can do for biologists in their research, for our better understanding of evolution, for helping us to communicate about evolution, etc. If a conceptualization does not appear to do any such work, it does not have a place in the toolkit; if it can do such work, its position in the toolkit is determined in relation to other conceptualizations that do similar work. In this context it should also be noted that a conceptualization does not have to do work in biological research: a conceptualization that for example is useful for communication about evolution in everyday contexts without having any role in biological science can still be included in the toolkit. An example, discussed in Sect. 3.1, is Darwinian fitness conceived as an organism’s metaphorical “lock-and-key” fit into its environment. This conceptualization does not play a role in biological research anymore, but is still very useful for understanding and communicating Darwin’s original theory as well as the basic idea of natural selection.

The toolkit thus is not a static entity that can serve as a fixed target for teaching, but rather a dynamic piece of material for educators and students to work with. Accordingly, the aim of science teaching cannot be that alternative conceptions should be "debunked" or "squashed" (Furtak, 2012; see Sect. 2) or replaced by the correct concepts. Rather, the aim should be to achieve a better understanding of scientific concepts by attempting to fit scientific and alternative conceptions into the slots in the toolkit – both success and failure with respect to fitting conceptions into the slots will yield an increased understanding of the state of affairs in the relevant area of science as well as the ongoing philosophical debate of the concepts involved. An extension of the toolkit with new slots to make a recalcitrant conceptualization fit, too, will yield such understanding, as it will show what this conceptualization can be used for.

In addition, the toolkit can be used to show important aspects of scientific practice and the nature of science more generally. I have argued that concepts serve as tools that often multiply as science progresses instead of old concepts simply being replaced by new ones, and that conceptual debates in science are not signs of confusion but rather of progress (progress with respect to improving and refining the tools scientists have for the task at hand). By relating students' alternative conceptions to slots in the toolkit more clarity can be achieved about how such conceptions relate to conceptions that were endorsed in the history of science but later moved out of focus as they were considered less useful, and to raise the question whether the conception might not still serve a role in research, communication, understanding, or elsewhere. As such, the toolkit motivates a more open interaction with students' alternative conceptions than a model on which those conceptions as misconceptions in need of replacement. In addition, I argued that a toolkit such as the one presented here can serve to highlight the extent of the conceptual diversity in a particular area of science to help students see that conceptual diversity is an intrinsic aspect of science.

As the suggested toolkit is deeply rooted in the results of work done in the history and philosophy of biology, it is an example of how history and philosophy of science can – and should – enter the science classroom. But examining conceptual debates is not only important when teaching biological subject matter to university-level science students or in high school biology classes. It is also crucial when teaching future teachers, who will have to address these debates with their students. In a sense, then, this paper is a plea-by-example for incorporating explicit history and philosophy of science components into teacher training programs.

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