Challenges with conceptualizations of evolution in biology education

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Project Overview

Teaching evolution as an interdisciplinary science

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Evolutionary theory in the 21st century has been embraced, albeit with varying degrees of controversy and consensus, across wide ranging disciplines. From biology and anthropology, to medicine, psychology, economics, sustainability science, computer science, and many more, core concepts of heritable variation and selection have been utilized by scientists across academia to understand change in the natural and social world. Evolution education, however, remains largely a disciplinary endeavor of biology education, and educators are left with little guidance on interpreting the broader interdisciplinary applications of modern evolution science discourse. This project takes a historical and sociological view on interdisciplinary conceptions of evolutionary theory and argues that, while legitimate scientific controversies abound, it is exactly these areas of controversy that may hold significant learning potential for addressing some of the persistent challenges facing evolution education more broadly.

In this article (Hanisch & Eirdosh, 2020c), we review some examples of current evolution education discourse, educational materials, and assessment tools that represent a number of challenges regarding how evolution is frequently conceptualized in evolution education. In Hanisch & Eirdosh (2020a) we provide evolution educators with a short review of how evolutionary concepts are conceptualized more broadly based on current discourse in evolution science. In Hanisch & Eirdosh (2020b), we outline a set of hypotheses about the educational potential of teaching evolution from a more generalized, interdisciplinary conception, addressing a range of enduring challenges in evolution understanding and acceptance. Based on the outlined challenges to evolution understanding and acceptance hypothesized to stem from a gene-focused conceptualization, together with the outlined opportunities hypothesized to be capable of addressing these challenges through teaching evolution from a more generalized, interdisciplinary conceptualization, we propose that the evolution education community should focus more strongly on investigating these avenues. In Eirdosh & Hanisch (2020d), we address a range of possible or existing objections that might hinder the advancement of such a research program.

Abstract

Evolution education is, by default, the domain of biology education, and as such, historical conceptions of evolutionary change drawn from the Modern Synthesis strongly influence our conceptualization of what evolution is and how evolutionary analyses are to be conducted. There is a surface logic to this influence, however, it abstracts out a robust interdisciplinary scientific discourse that has been particularly productive during the 21st century. The continued conceptualization of evolution from the idealized, gene-centric, Modern Synthesis model may be problematic in terms of evolution understanding and acceptance. In this article, we take a closer look at some examples of current discourse, standards, educational materials, and assessment tools of evolution education and point out a number of challenges regarding how our field tends to frame the evolutionary analysis of, especially, human-related traits of behavior, cognition, and culture.

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Introduction

Conceptual advances in evolution science suggest the possibility that evolution could and perhaps should be taught as an interdisciplinary science (Hanisch & Eirdosh, 2020a). At the same time, evolution education continues to struggle with a range of persistent problems of evolution understanding and acceptance among students and the general public (Barnes et al., 2017; Gregory, 2009; Heddy & Sinatra, 2013; Legare et al., 2018; Pobiner, 2016; Rosengren et al., 2012; Sinatra et al. 2008). In Hanisch & Eirdosh (2020b), we argue that these persistent problems may be linked, albeit in complex and as yet not fully understood ways, to the persistence of gene-centered as opposed to trait-centered, interdisciplinary approaches to evolution education. In this article, we review a range of examples across evolution education standards, assessment tools, and classroom materials that illustrate this persistence of gene-centered conceptualizations and resulting challenges.

Evolution education has been predominantly informed by the conceptualization of evolutionary theory called the Modern Synthesis (MS). This framing of evolutionary change provided a core set of concepts and principles that have defined evolution education discourse, materials and assessment tools in the last decades and to this day. These concepts and principles do provide a solid basis for some core understandings about how evolution operates in many cases. However, advances in various branches in biology and in disciplines outside of biology have revealed that the evolutionary change of organisms, populations, and ecosystems is often much more complex than previously thought, and that evolutionary concepts can be applied to a much broader set of evolving complex adaptive systems besides biological populations of organisms (see Hanisch & Eirdosh, 2020a, for an overview). These insights are especially relevant in regards to the past and future evolution of our own species.

If we step back from the current norms and conceptualizations of evolution education as it is widely practiced today, and instead take a broader view of the full landscape of evolution science and education as a whole, we can begin to see how the current framing of evolutionary change in our field may be driving the persistent challenges we struggle to make progress on (Fig. 1), and tends to prevent engagement with perspectives in 21st century evolution science.

In the following sections, we argue and show that the current approach in evolution education entails an implicit transfer of an idealized (gene-centric) model of evolution to the teaching and learning about all biological phenomena, including human behavioral, cognitive and cultural traits. This idealized, gene-centric conceptualization thus tends to invite or even encourage problematic reasoning, and leads to unclear or conflicting framings of core evolutionary concepts. We also argue and show that the current approach in evolution education appears to not embrace the opportunity of helping students and teachers engage in critical reflection on the transferability of core evolutionary concepts both within and outside the biological domain. This is problematic both from a scientific and pedagogical point of view. We suggest the remedy is to engage students in understanding the differences between gene-centered and

trait-centered models of evolutionary change, and the relative transferability of concepts within and across these theoretical frameworks.

Fig. 1. Persistent challenges to evolution understanding and acceptance and hypothesized contributions of a gene-centered approach in sustaining or exacerbating, rather than overcoming, these issues. See Hanisch & Eirdosh (2020b) for details.

Implicit transfer of an idealized gene-centric model

One area of conceptual difficulty that we have identified in Hanisch & Eirdosh (2020b) is the degree to which a gene-centric model of evolution pervades the framing of evolutionary concepts and choice of biological examples in such a way that it remains difficult to apply this conceptualization to areas of more complex evolutionary dynamics, including to the evolution of behavioral, cognitive and cultural phenotypes, particularly relevant in our own species. Yet such applicability of these idealized notions of evolutionary change to *all* areas of biology is often implied or even made explicit and encouraged, leading to problematic reasoning about evolutionary change in general. Furthermore, the attempt to apply such idealized conceptualizations across all phenomena appears to lead to unclear and sometimes conflicting framings of concepts within materials.

Evolution education materials and assessment tools tend to focus on examples of non-human animals and morphological or physiological adaptations whose evolutionary explanation does not require more complex causal dynamics, such as the role of goal-directed organism behavior, developmental processes, or complex reciprocal interactions among living things or between living things and their environment. There is a certain and potentially justifiable logic to starting with simplicity and moving towards complexity (though this logic is also refuted, see Fuentes, 2020; Jamieson & Radick, 2017), but even if this logic is accepted, it must be engaged with caution and nuance.

We argue that this tendency to focus on idealized evolutionary dynamics as applied to special cases, may prove difficult if such idealization is thought to represent “the truth” and to apply to all evolutionary explanations of observable traits. As Baedke et al. (2020) point out, standard conceptualizations of evolutionary theory stemming from the MS present *idealizations*, abstracting out developmental processes and proximate interactions. Such idealizations then influence the choice of model organisms for which these idealizations hold, such as organisms with “invariant body plans, low levels of developmental plasticity, and ease of genetic manipulation” (Baedke, et al., 2020). Especially when it comes to understanding human evolution, the transfer of such idealized models becomes significantly problematic.

Below we provide examples of this trend from evolution education standards, assessment tools and educational materials.

Evolution education standards

Within evolution education standards, we find that concepts and principles of evolution are sometimes variably or inconsistently defined and presented to students. Here we highlight examples from the Next Generation Science Standards (NGSS; Achieve, 2013), the Understanding Evolution conceptual framework (University of California Museum of Paleontology, 2009) and the core concepts provided by Brownell et al. (2014). We suggest that this underlying lack of clarity further prevents engagement with 21st century perspectives on trait-centered models of evolution.

Next Generation Science Standards

The Next Generation Science Standards (NGSS) were developed to bring 21st century scientific skills into the US science education curricula. We generally applaud this effort but also find some problematic conceptualizations when it comes to evolution science.

First, in relation to human evolution, it should be noted that the NGSS specifically excluded behavioral and social sciences from its definition of “science education” (National Research Council, 2012, pp.13-14). Thus, on the whole, when students and teachers seek to explore causation in human evolution, they are likely to be left without a well-developed conceptual

toolkit for understanding the role of behavioral, cognitive, and cultural traits as drivers of evolution in our species.

Further, we find some unclarity within the NGSS regarding the relative roles of competition versus cooperation in evolution more broadly. Within the NGSS disciplinary core idea of Adaptation, we find the following:

“Evolution is a consequence of the interaction of four factors: (1) the potential for a species to increase in number, (2) the genetic variation of individuals in a species due to mutation and sexual reproduction, (3) competition for an environment’s limited supply of the resources that individuals need in order to survive and reproduce, and (4) the ensuing proliferation of those organisms that are better able to survive and reproduce in that environment.”

In contrast, in the NGSS topic of ecosystems it is stated that “some animals form groups that help members survive.”; and in the disciplinary core idea “social interactions and group behavior”: “Group behavior has evolved because membership can increase the chances of survival for individuals and their genetic relatives.”

In other words, evolution is foundationally defined as organism-level competition among genetically variant phenotypes, without an emphasis of the possible roles of coevolutionary dynamics including social interactions, as it seems to not fit into this idealized framing of how evolution operates. The role of the latter in driving evolution is thus not emphasised or even missing under the umbrella of evolution, yet mentioned elsewhere in the standards without a clear relationship between these two conceptualizations.

A stronger focus on the evolution of cooperation at multiple levels of organization, in other organisms, and especially in our species, may provide opportunities for students to consider the roles of *both* competition and cooperation in evolution, thus countering some of the perceived “ruthlessness” of evolution (see Hanisch & Eirdosh, 2020b).

Understanding Evolution conceptual framework

The *Understanding Evolution conceptual framework* (University of California Museum of Paleontology, 2009) was developed by a group of experts seeking to clarify and expand a learning progression of core evolution concepts for the K-16 grade levels. The following examples highlight how the framework appears, on the one hand, to reinforce a simple and direct genotype-phenotype relationship, and on the other hand, it is inconsistent regarding what levels of organization natural selection acts on.

In the “Mechanisms of evolution” section of the framework, we find statements like “Evolution results from selection acting upon *genetic variation* within a population”; “Natural selection acts on *phenotype* as an expression of genotype”; “Phenotype is a product of *both genotype and* the organism’s interactions with the *environment*” (emphases added). Experts in evolution science may be capable of interpreting the intended logic behind these statements, but especially for novice learners, this inconsistent framing of both the level on which selection acts and the very

definition of the phenotype concept is very likely to drive confusion and provide obstacles to the engagement with modern scientific perspectives on the complex causation of phenotypes.

In the 12-16 grade level, we find the item that “Natural selection is capable of acting at *multiple hierarchical levels*: on genes, on cells, on individuals, on populations, on species, and on larger clades.” (emphasis added). In another instance, it is stated that “Populations, not individuals, evolve.” This is inconsistent. If natural selection is said to be able to act on multiple levels including genes and cells, how can it be that only populations (with the implication that what is meant is populations of individual organisms) but not individual organisms (as populations of cells and traits) evolve? A generalized and transferable understanding of the *population* concept, as is commonplace within trait-centered evolution models (see Hanisch & Eirdosh 2020a for expanded discussion), would help resolve this confusion.

Only at the 12-16 grade levels is a definition of evolution offered, namely that “Evolution is often defined as a change in allele frequencies within a population.” The term “often” is interesting in this regard, as it implies that there are also other - apparently non-problematic and scientifically valid, yet unidentified - definitions of evolution in use. We suggest that evolution educators should not just hint at these multiple definitions (indeed, multiple conceptions), but should explicitly engage students in reflecting on the similarities and differences between gene-centered and trait-centered models of evolution.

A number of authors have emphasised that engagement and interest in evolutionary theory may be increased by pointing out to students the relevance of evolution to their lives. However, a gene-focused conceptualization of evolution constrains the examples that are often given regarding the relevance of evolution in everyday life and in society. For example, the Understanding Evolution conceptual framework states, regarding the relevance of evolution, “As with other scientific disciplines, evolutionary biology has applications that factor into everyday life, for example in agriculture, biodiversity and conservation biology, and medicine and health.” Similar themes are pointed out by many other authors (e.g. Pober et al., 2018). While these are important areas that can highlight to students how evolutionary biology is relevant for their everyday lives, important other areas such as understanding the evolutionary and developmental causes of human behavior, culture and cognition, are notably absent from this list. As we point out in Hanisch & Eirdosh (2020b), this may well have to do with the fact that such human traits do not have simple, linear, underlying genetic causes, meaning that they do not fit neatly into the idealized understanding of evolution, and they may even appear outside the realm of traditional STEM fields, and thus do not fit neatly into one of the traditional subject areas. In this regard, since evolution education standards usually address evolutionary *biology*, more interdisciplinary perspectives of evolutionary change such as in the domain of culture, may be considered outside of the scope of the standards. However, given the centrality of behavior, cognition, and culture in our species history and everyday lives, this may impede cultivating student appreciation of evolutionary theory more generally, especially as it pertains to human evolution.

A similar problem concerns the methods and lines of evidence for evolution that tend to be highlighted in standards. For example, in the Understanding Evolution conceptual framework, under “Our understanding of life through time is based upon multiple lines of evidence.”, specific lines of evidence that are listed in the 9-16 grade levels include similarity of DNA, anatomical features, and developmental evidence to infer the relatedness of taxa; fossils and their distribution and related physical, chemical, and geological evidence, experimental evidence to study evolutionary processes, and artificial selection. Interestingly, experimental and observational evidence stemming from behavioral science and psychology, such as cross-species and cross-cultural comparisons, are lacking from this list, yet they are critically important areas of inquiry in evolutionary biology and particularly evolutionary anthropology, and may be of particular interest to students.

Core concepts for undergraduate biology

Brownell et al. (2014) created a guide for core concepts in biology for undergraduate biology education, and defines as an overarching principle for the concept of evolution that “Species evolve over time, and new species can arise, when *allele frequencies* change due to mutation, natural selection, gene flow and genetic drift.” (emphasis added). On the other hand, the overarching principle for the core idea of systems is that “Biological molecules, genes, cells, tissues, organs, individuals, and ecosystems interact to form complex networks. A change in one component of the network can affect many other components.” Complex interactions and change in biological systems are emphasized in this instance, but these dynamics are notably deemphasized or lacking in the framing of evolutionary change within the same standards. Again, experts in biological evolution may be able to resolve the intended logic of these claims, but for novice learners such as students (and perhaps some teachers), this is likely to leave fundamentally unresolved questions such as: are changes in these complex networks of interaction considered “evolution”, and if not, why are only certain kinds of changes, or certain affected components (e.g. alleles), considered to encapsulate evolutionary change? We argue that a trait-centered understanding of natural selection as resulting from reciprocal, distributed interaction in biological *systems*, allows a more explicit integration of the concept or core idea of “system” in the biology classroom (see Hanisch & Eirdosh, 2020a,b).

The kinds of conceptual unclarity we have outlined in these three influential standards above are largely representative of the milieu of mixed messages and unresolved, often contrasting definitions that students and teachers are left to navigate. This is problematic in its own right, but becomes particularly troublesome when default assumptions about gene-centric models are used to assess student understanding, as we outline in the following section.

Evolution understanding assessment tools

Gene-centric idealizations and the resulting choice of case studies seem to also have greatly influenced the development of evolution understanding assessment tools. In a review of concept inventory assessment tools for evolution, Furrow and Hsu (2019) found that the topics of evolution of behavior, human evolution, sexual selection or coevolution have rarely or not at

all been covered in currently existing tools. For example, Kalinowski et al. (2016) state explicitly that their assessment tool for understanding natural selection (Conceptual Assessment of Natural Selection - CANS) does not include “questions on advanced topics such as sexual selection, evolutionary constraints to adaptation, or the molecular basis of evolution”. Legare et al. (2018) point out that “Current methods for assessing students’ understanding of evolution are grounded in the evolution of non-human animals and non-mentalistic traits. (...) social scientists may well need their own assessment tools—tools capable of gauging students’ understanding of the evolved nature of human cognition and human behavior.”

Table 1 features some examples of how items in common assessment tools reflect this problematic idealization, especially how it is implied that these idealizations hold across the board in biology, including in the domain of human behavior.

Particularly the assessment tool developed by Nettle (2010) seems noteworthy in this regard, as it is specifically targeted towards an appropriate understanding of the evolution of human traits. Legare et al. (2018) note that “Nettle’s [2010] assessment does not, however, cover the evolution of human cognition or human behavior, and it remains an open question how to probe such topics authentically and systematically.” In fact, the questionnaire clearly included examples of human (and animal) behavior, but seems to not adequately include perspectives of evolutionary anthropology and human behavioral science, particularly the role of social learning and the evolution of cooperation in our species (see table 1). The notion of “soft inheritance” is invoked and framed as a misconception, which seems to inadequately address the significant role of social learning in affecting the distribution of behavioral variation in many species, including our species (e.g. Hoppitt & Laland, 2013). Furthermore, the assessment item that is meant to target the concept of inclusive fitness, presents two choices (see table 1) between individual and whole species, which force on students the notion that humans are mainly selfish fitness-maximisers. This notion is encapsulated in the *Homo oeconomicus* model of human behavior that has been prevalent in economics and is now widely considered outdated and inadequate (e.g. Henrich et al., 2005). The two options do not take into account the wealth of behavioral science research showing that humans quite often behave in prosocial ways, that is, not merely in a way “as to gain the maximum benefit for *his or her self*” (but also not necessarily in a way as to benefit the whole species). In fact, none of the two choices encapsulate the targeted concept of *inclusive fitness* - which entails behaviors that do *not* necessarily or exclusively result in the maximum benefit to the organism performing the behavior, but also to others in the group who are affected by the behavior, such as related others or cooperating, reciprocating members of social groups. Students are left with no option to adequately reason about the role of inclusive fitness in the evolution of human social behavior.

Table 1: Example features and items in common assessment tools for evolution understanding that we consider problematic in terms of how they idealize across examples and contexts or misrepresent current scientific conceptions.

Assessment tool, reference	Selected examples	Comments
Conceptual Inventory of Natural Selection (CINS; Anderson et al., 2002)	Concept of heritable variation - distractor item: <i>"Traits acquired during an organism's lifetime will be inherited by offspring"</i>	A significant constituent of biologists would agree that one type of trait, namely learned behaviors, are by definition "acquired" during an organism's lifetime and are often passed onto offspring in many species through the transmission mechanism of social learning (e.g. Hoppit & Laland, 2013; Jablonka & Lamb 2006).
	Concept of change in a population - distractor item: <i>"Learned behaviors are inherited"</i>	
	Concept of origin of variation - only mutations feature in the correct and distractor explanations	This reinforces or implies the notion that organisms (including humans, including their behaviors and cultures) only vary based on genetic differences, leaving out other sources of phenotypic variation.
	Concept of limited survival - distractor item: <i>"organisms work together (cooperate) and don't compete."</i>	This seems to present a false choice as it reinforces or implies the notion that cooperation does not happen in nature or that it can not evolve. Cooperation and competition can (and do) happen at the same time in many populations, particularly in our species.
	Context examples: Galapagos finches and the traits of beak size and shape; guppies and the trait of skin coloration; the evolution of three Canary Island lizard species from an African ancestor, with test questions covering a variety of traits.	There is a focus on morphological traits in the examples, but then multiple choice items include behavioral traits as if they can be reasoned about in the same way as morphological traits.
Assessing COntextual Reasoning about Natural Selection (ACORNS, Nehm et al., 2010, 2012)	The tool includes a choice of case examples by different variables, including type of trait - however, only a distinction between <i>"Immunity/resistance vs. other trait changes"</i> is made because <i>"Immunity and resistance are unique reasoning contexts that elicit naive ideas about "adapting" "</i>	"Other trait changes" lumps all traits into a category as if they are caused the same way, when instead, different traits may evolve in a population through different causal interactions between factors or may involve different mechanisms of variation, selection and inheritance (see also Hanisch & Eirdosh, 2020a, e), or may involve differing roles of developmental processes vs. natural selection (Love, 2013); particularly a distinction between morphological and physiological vs. behavioral/cognitive/cultural traits seems crucial.
	<i>"How would a biologist explain how trait X evolved?"</i>	This reinforces the notions that (a) all traits can be explained the same way, and (b) all biologists will explain a trait the same way.
Nettle (2010) - assessment of student understanding using human examples.	Targeted misconception: <i>"Soft inheritance: The idea that if one individual learns to swim, swimming ability thereby becomes a species-wide characteristic"</i>	"Soft inheritance", i.e. inheritance streams beyond genetic such as social learning, are legitimate mechanisms of trait transmission in many species, particularly in humans (e.g. Hoppitt & Laland, 2013)
	Targeted misconception: <i>"The expectation that behaviors which are for the good of the species will be prevalent rather than those which maximize inclusive fitness.": "How, in general, would you expect a person to behave? A) In such a way as to benefit the species; B) In such a way as to gain the maximum benefit for his or her self."</i>	This presents a false choice between individual and whole species, abstracting out the multi-level group structures that shaped human evolution, and reinforcing the notion of humans as rational and selfish fitness-maximisers (Homo oeconomicus). None of the two choices in fact encapsulate the targeted concept of inclusive fitness.

Overall, it appears that assessment tools aim towards carving out and presenting an idealized and clean picture of evolution as if this is how biologists generally, and across contexts, reason about the evolution of traits, when in reality, the scientific discourse is much more diverse and nuanced across the many biological subdisciplines. As Love (2013) points out, one key pedagogical implication from the interdisciplinary field of evo-devo is that “Reasoning in biological science is not homogeneous; biological science is composed of multiple perspectives that correspond to diverse explanatory aims and exhibit divergent reasoning styles. We must teach the heterogeneity of reasoning in biology”.

Evolution education materials

Idealized examples of evolutionary change have also greatly influenced the research and development of evolution education materials and teaching strategies. In a review of research that may add to teachers’ pedagogical content knowledge on evolution education, Ziadie and Andrews (2018) found that topics such as the evolution of behavior, sexual selection and coevolution have received relatively little or no attention in educational research for undergraduate and secondary school biology teaching.

As an example, consider the chosen themes within the Teaching Evolution Through Human Examples project (Pobiner et al., 2018) - adaptation to high altitude, skin color, and resistance to malaria. All examples within this project cover morphological and physiological traits with a clear genetic basis, or which allow explanations of natural selection that do not entail more complex causation. Another unit within this project, which was not implemented in the study by Pobiner et al. (2018), was called “What does it mean to be human”. In this unit, the focus was primarily on phylogeny, genetics and archeological concepts (Smithsonian Institution, 2015). In the final project of this unit called “Explaining Human Characteristics”, students are expected to provide evidence and create scientific explanations on the evolution of a chosen human trait from a list including increased brain size, a longer childhood, cooking, language, and the ability to create technologies (Smithsonian Institution, 2015, p. 47 ff.). However, important concepts like social selection, cooperation, social learning, niche construction, gene-culture coevolution, or important lines of evidence such as comparative, developmental and cross-cultural behavioral research, which are commonly invoked by evolutionary anthropologists to explain the evolution of such complex traits in our lineage (e.g. Burkart et al., 2009; Hayes & Sanford, 2014; Laland et al., 2010; Morgan et al., 2015; Street et al., 2017; Whiten & Erdal, 2012), are not included in the unit.

Another example that illustrates how idealized concepts of evolution are implied to be sufficient to explain the human condition, is a Massively Open Online Course (MOOC) developed by geneticist and evolution education researcher, Laurence Hurst, and colleagues (University of Bath, 2020). This MOOC is informed by Hurst’s work in advancing the notion that to increase understanding (though not acceptance) of evolution, educators should “teach genetics first” (Mead et al., 2017). The online syllabus follows this logic, starting with the mechanistics and central tenets of exactly the gene-centric idealized model of evolution we describe. Then, in the

final unit on “Human Evolution”, learners are presented with archaeological evidence of the historical rise of humans, but not given any additional conceptual tools for understanding the multiple evolutionary streams of inheritance that are widely recognized as driving the evolution of our species.

A final example from evolution education teaching materials can further make clear the problematic nature of a gene-centric conceptualization. Regarding the educational value of reflecting on future human evolution, Andrews et al. (2011) report on an intervention to teach natural selection through the question “Are humans still evolving”? The intervention sought to draw students’ attention to the three necessary components of evolution by natural selection of trait variation, trait heritability and differential reproduction. Within the intervention, these concepts were defined from a gene-focused conception, and these conceptions are then used to reason about the evolutionary change of traits whose distribution and spread may be caused through a much more complex set of factors and processes besides genes and natural selection through differential reproduction.

Let us consider the example discussed in Andrews et al. (2011) on whether humans are *evolving* to become more obese, a trait that was proposed by students, presumably because they are aware of the spread of this trait in society. Looking at how student answers are interpreted (e.g. as misconceptions) and how classroom discussions are guided, the question on whether the change or spread of certain human traits can be considered the result of evolution (and therefore, whether students correctly apply evolutionary thinking to explain observed changes in trait frequency), depends crucially on how one defines concepts such as “inheritance” and differential reproduction or “fitness”.

The following is an excerpt from a classroom discussion (Andrews et al., 2011, supplemental materials) to help students explore whether humans are indeed *evolving* to become more obese:

Instructor: “Is weight or tendency to put on extra weight heritable?”

Students: “Probably, but I don’t know. I mean you see whole fat families, so probably it’s genetic.”;

“Yeah, but families also all eat unhealthy or sit around all day, so maybe they just got fat because of that and not because of their genes.”

(...)

Instructor: “Assuming it is heritable, do you think fat people are having more children than thinner people?”

Student: “Umm...no, I guess not.”

The conclusion that students are meant to have drawn from this discussion is that humans are not evolving to become fatter, because on the one hand, it is questionable whether this trait is purely genetically inherited, and on the other hand, it is questionable that obese individuals have more offspring than other individuals. The discussion concludes with the question “What are some other explanations for why more people are obese?” (Andrews et al., 2011, supplemental materials).

However, such classroom discussions may be more constructive for evolution education by, on the one hand, considering a variety of possible mechanisms of inheritance thus reinforcing a transferable notion of trait transmission as important in changes of phenotype frequency, and on the other hand, by relating the topic fruitfully to issues of public health in human populations, which can help make students be more aware of the role of evolutionary thinking for addressing real world problems. Thus cultural evolution scientists (e.g. Mesoudi, 2011; Richerson & Boyd, 2005; see Hanisch & Eirdosh, 2020a) would consider that obesity may spread in a human population not primarily through differential reproduction and genetic inheritance, but possibly through ecological inheritance of environments rich in fatty and sugary foods, or of environments that present little incentive for, or even impediments to, regular exercise. In this context, the concept of evolutionary mismatch might also be fruitfully engaged. Cultural evolution scientists would further consider that behavioral traits like dietary habits (which can in turn bring about changes in other phenotypic traits such as obesity) can be transmitted through mechanisms of social learning, and not only vertically from parents to offspring, but also horizontally and in an oblique manner to others in the population. These mechanisms were indeed pointed out by students in Andrews et al. (2011, see quote above) as possible explanations for the transmission or spread of obesity within a family. But these considerations were not considered to be relevant for an evolutionary account, and hence not viewed as relevant to the learning goals for this particular lesson activity, foregoing the opportunity to have classrooms engage in current public health issues while cultivating student understanding of evolutionary concepts in a more nuanced and transferable fashion.

To summarize this section, evolution education standards, assessment tools, and materials use idealized notions of evolutionary concepts and biological examples, and tend to not explicitly integrate concepts such as coevolution, niche construction, social learning, sexual selection, evolution of cooperation, or the role of behaviors and developmental processes in bringing about phenotypic variation. These concepts are often treated as add-ons or special cases to this gene-focused conception of evolution, rather than integrated under a generalized umbrella of evolution (see also Hanisch & Eirdosh, 2020a, fig. 1). This may introduce or exacerbate challenges related to student understanding and acceptance of evolution, particularly regarding our species, or the sense of relevance of evolution to everyday experience.

Lack of critical reflection on the transfer of core evolutionary concepts

A related set of challenges that we have identified (see Hanisch & Eirdosh, 2020b) and would like to highlight in this article relates to how evolution education scholars attempt to deal with students' intuitive ideas or everyday understandings of evolutionary concepts and how the transferability of such concepts across various domains is approached (fig. 1). This issue is central to the pedagogical implications of navigating the relative value of gene-centered versus trait-centered models in evolution education.

For example, a dichotomy is sometimes created between the “everyday use” of the term evolution vs. “biological” evolution. Van Dijk & Reydon (2010) explain that *“In everyday contexts, ‘evolution’ is often used to refer to a variety of processes of change in time: languages, societies, cities, culture, the economy, the universe, technology, car models, etc. all are commonly said to evolve”; “In biology, in contrast, ‘evolution’ (...) is used to denote the particular type of change process that populations of organisms undergo.”* Similarly, Andrews et al. (2011) point out that *“When asked if humans are evolving, students often equate change they see in the human population with evolution.”*

In contrast to this dichotomy, many scientists such as those studying *cultural evolution* in fact understand and study the evolution of cultural traits - including languages, societies, cities, culture, the economy, technologies - in similar ways as biologists studying the evolution of other traits in the biological world (e.g. Mesoudi, 2011; Mesoudi et al., 2006; Richerson and Boyd, 2005; Richerson and Christiansen, 2013; see Hanisch & Eirdosh, 2020a, for an overview). They do this by *critically transferring* the concepts and processes of biological evolution to the domain of culture.

In the German biology education context, the theme of cultural evolution in fact appears in some state curricula and is covered in more or less depth in some biology textbooks. For example, in some German biology textbooks in the section on human evolution, we find paragraphs such as:

“Principally there are two mechanisms of transmission of information: genetic inheritance and learning from a model.” (Jaenicke & Paul, 2004, p. 435, own translation)

“In contrast to biological evolution, cultural evolution enables the transmission of acquired traits.” (Baack et al., 2016, p. 493, own translation)

“In many animal species, parents pass their acquired knowledge and skills on to their offspring - generating traditions and cultures. In humans the transmission of experience is especially elaborated. (...) The transmission of acquired traits from generation to generation, the imitation of behavior from models, learning and teaching - all this is summarized under the term of cultural evolution. Humans are influenced by it to a similar degree as by natural evolution. (...) Cultural and natural evolution have a number of similarities. Attractive, new ideas or fashions spread in populations with a similar dynamic as alleles.” (Markl, 2018, p. 337, 338, own translation).

Students that learn about this generalized notion of evolution as it can be applied both to cultural *and* genetic variation, might choose answers on standardized evolution understanding assessment tools (see above section, table 1) that would be evaluated as “wrong” from a gene-centric perspective, such as responses concerning the heritability of acquired traits.

Critically, the latter textbook quoted above then goes on to reflect on the future of human evolution. In answering this question, the text falls back to a gene-focused definition of evolution: *“Of course we are still subjected to the evolutionary mechanisms like mutation, selection, gene drift and gene flow through migration (...) Hence, the evolution of humans continues.”* (Markl, 2018, p. 339, own translation). No further guidance is given in the book on

how to navigate this changing use of the term evolution and the concept of trait transmission, or on how to reflect on the importance of cultural evolution of our species in the future. This aspect is also related to the unclarity and inconsistency in education materials on how to define and reason about evolutionary concepts (see section above).

Evolving the future of evolution education

How can evolution education advance in order to resolve inconsistencies and the proliferation of rather idealized conceptualizations of evolutionary change? It is important to emphasize that some developments are already leading the way.

Regarding the question of embracing more complex causal accounts of the evolution of traits, from a pedagogical point of view, one might argue that such accounts are too advanced and that it is better to start with simple and idealized examples, and then advance to more complex concepts and examples in later years or advanced courses. However, an emphasis on such idealizations may ultimately hinder the development of evolution understanding and acceptance (fig. 1). As Jamieson and Radick (2017) pointed out in their report on a genetics course that de-emphasised simple and linear genotype-phenotype relations, the “simple-to-complex trajectory, for all its abundant virtues, runs the risk of creating students who cling to the simple (...). Instead (...) our students were introduced to the complexity of genetic influences in the first lecture.” We argue that this aspect of “leading with complexity” (Fuentes, 2020) can and should also be applied to evolution thinking and may help overcome various persistent challenges in evolution education (see Hanisch & Eirdosh, 2020b). From a pedagogical view, it is also important to emphasise that leading with complexity in the evolution classroom does not need to be a complex matter in itself - various teaching tools such as causal maps (see Hanisch & Eirdosh, 2020e) and computer simulations are available to teach students the complex nature of evolutionary change, from the start, with relatively simple models.

The examples of German textbooks quoted in the previous section, explicitly highlighting the transferable nature of evolutionary concepts to the domain of culture, also indicate that a shift is already underway in terms of “opening” up and expanding upon the idealized nature of gene-centric evolution in evolution education. Building on these developments, we argue that the focus now needs to be on helping teachers and students to adequately transfer between these different conceptualizations, e.g. with the help of analogy maps (see Hanisch & Eirdosh, 2020b, table 3 and supplementary materials), and applying them appropriately to the explanation of various traits.

Finally, evolution educators should consider expanding our conceptions of the currently limited lines of evolutionary evidence (e.g. genetics, paleontology, archaeology) to more explicitly include behavioral, cognitive, and cultural sciences, for exploring the evidence and scientific methods of evolutionary anthropology in the classroom. Again, we find one (single) example in a German highschool biology textbook (Bayrhuber et al., 2005, p. 509) leading the way - a game theoretic experiment that investigated facets of human altruism (Fehr & Gächter, 1999).

However, this is the only example of a behavioral experiment within the section on human evolution that we found in our sample of 15 prominent German biology textbooks (unpublished data). We argue that the wealth of cross-species, developmental, and cross-cultural behavioral experiments produced in recent decades within the sub-fields of evolutionary anthropology, greatly advancing our scientific understanding of what it means to be human, likewise presents an untapped source of nature of science lessons as well as a source for insights into the role of behavioral variation, culture, and social learning in the evolution of our species. These insights can not be provided by genetics, paleontological, and archeological evidence alone.

Conclusions

Is the evolution education community prepared to incorporate the recent developments in interdisciplinary evolution science in the future? The examples highlighted in this article indicate that it might be time to revisit some commonly held wisdom about the meaning of core concepts and processes in evolution as inherited from the formulation of the Modern Synthesis. This is because on the one hand, commonly held idealized definitions are inviting some inconsistencies and unclarities within standards and materials about what evolution *is*, and on the other hand, evolution education might be closing itself off from important learning opportunities provided by more interdisciplinary perspectives.

While the often cited mantra “Nothing in biology makes sense except in the light of evolution” (Dobzhansky, 1973) has been expanded among scientists to other phenomena such as culture, society, and economics (see Hanisch & Eirdosh, 2020a), Kalinowski et al. (2010) go in the opposite direction, with the aim to advance evolution education, and state that “Nothing in Evolution Makes Sense Except in the Light of DNA”. We and many others in evolutionary anthropology would take issue with this claim. General evolutionary dynamics can be understood without understanding the mechanistic details of DNA. This does not ignore the role of genetics in evolutionary processes, but only places these molecular ecosystems within the appropriate causal context of the complex evolutionary systems in which they are embedded.

Trait-centered perspectives have fully arrived at the highest end of evolution science. Trait-centered perspectives have already begun to be integrated into mainstream evolution education materials. We argue that it is time to build on these developments more explicitly, including in standards and assessment tools, as inconsistencies and problematic inferences will otherwise only become more serious, to the disadvantage of students and teachers.

Abbreviations

MS - Modern Synthesis

MOOC - Massively Open Online Course

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