

# Teaching for the interdisciplinary understanding of evolutionary concepts

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## Abstract

Evolutionary concepts are used, with varying and arguable degrees of scientific utility, across a wide range of disciplines. Evolution education, however, remains overwhelmingly within the confines of biology education, when it is taught at all within general education. The reasons for this disciplinary myopia are complex, and normative guidance for curriculum designers is scarce. This contribution explores how understanding the *structures of knowledge*, or the organization of facts and generalizations in science, cognition, and education, may help illuminate the educational potential and evidence-informed pedagogical practices appropriate for teaching about the interdisciplinary application of evolutionary concepts.

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## Introduction

Theoretical and methodological advances in evolution science suggest the possibility that evolution could and perhaps should be taught as an interdisciplinary science (Hanisch & Eirdosh, 2020a). However, such a potential generalization of evolutionary theory, as also explored in this volume, is perhaps among the scientific developments that most challenge the current structure of educational curricula and educational research and practice. While science is always advancing with emerging fields, theories, methods, and findings, and while curriculum development efforts often attempt to integrate these developments into school curricula, it appears that the generalization of evolutionary theory puts a particular strain on the structure of the educational system that has been forged over the second half of the 20th century.

Evolution education has been predominantly informed by the conceptualization of evolutionary theory known as the Modern Synthesis (MS). This framing of evolutionary change provided a core set of concepts and principles that have defined evolution education discourse and research, curriculum structure, materials, and assessment tools in the last decades, and presently. While it can be argued that these concepts and principles do provide a solid basis for some core understandings about how evolution operates in many cases, they may also present constraints in relation to broader educational goals.

In our educational design work, we regard a transferable understanding of evolutionary concepts and processes as a core set of learning goals for students to understand themselves, their fellow humans, their human-made world, as well as problems and solutions to sustainable development. In this work, we have been informed by three emerging fields of discourse: discussions around the possible value of an *Extended Evolutionary Synthesis* (EES), the emerging field of *Cultural Evolution Science* (CES), and the tradition of behavioral sciences known as *Contextual Behavioral Science* (CBS). To our knowledge, with some exceptions (e.g. Apodaca et al., 2019; Arújo, 2020; Pugh et al., 2014), the conceptualizations emerging from within and across these areas appear to be not currently part of the broader discourse on how to teach evolutionary science, particularly in secondary school and general education more broadly.

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 (2020a), 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. That is, we suggest that defining the process of evolution solely in terms of changes in allele frequencies (as opposed to changes in trait frequencies) within a population presents significant constraints to solving the persistent problems of the evolution education field. Said another way, we argue that the constrained rather than generalized framing of core evolutionary concepts may be constraining our search for solutions to the challenges of evolution education.

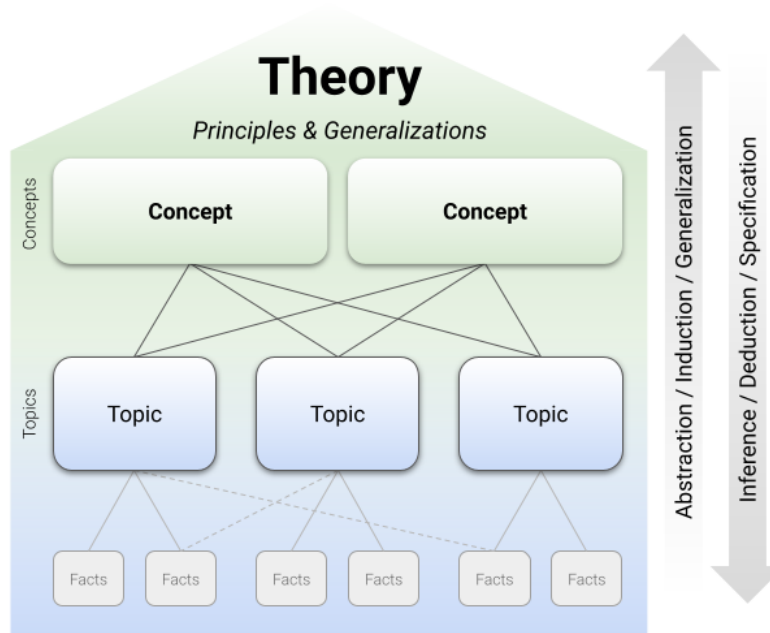
Here, we build on this argument to clarify the role of structures of knowledge in science, cognition, and evolution education, and the relationships between them. This clarification suggests that critical reflection on the generalizability and contextually specific application of evolutionary concepts is a central yet underutilized pathway to deeper public understanding of evolution as an interdisciplinary science. Thus, teaching approaches that target the development of conceptual understanding and transfer of learning should take on a more central role in the evolution educator's toolkit. In Box 1 (p. XX), we take an excursion into the

related field of complex systems science to see how domain-general concepts and processes of complex systems, and the learning goal of systems thinking, have already made their way into curricula. We argue that generalizable evolutionary concepts and the learning goal of evolutionary thinking can and should be equally considered as central in 21st century education.

In the sections that follow we unpack what is meant by *structures of knowledge* across the domains of science, cognition, and evolution education. We then highlight a range of implications for curriculum and instructional design of a generalized evolutionary theory.

## Structures of knowledge in science, cognition, and evolution education

Overall, educators, scientists/philosophers of science, and cognitive scientists think of knowledge as structured, from concrete facts, events, examples or phenomena, to more and more abstract concepts, to hypotheses, generalizations, and principles linking several concepts, and finally a body of theory (fig. 1). In relation to this, educators, scientists and cognitive scientists also regard concepts, conceptions, and analogies as playing central roles in building structures of knowledge from existing prior knowledge. One of the indications of the interdisciplinarity of this view of knowledge, is the use of Bayesian causal inference models in both philosophy of science and cognitive science, which link causal hypotheses on different levels of generalization with inferences and evidence (e.g. Baraghith & Feldbacher-Escamilla, 2021; Gopnik et al., 2004; Gopnik & Wellman, 2012; Goodman et al., 2011).



**Fig. 1.** Basic structure of knowledge, highlighting the relationships between concrete facts, topics, generalizable concepts, generalizable principles and finally theory. Based on Erickson et al. (2017).

## Structures of knowledge in science

As the contributions of this volume show, the debate around a generalization or extension of evolution beyond the domain of biology often revolves around the assumptions and implications regarding the structure of evolutionary theory as a whole, and the role that different conceptualizations and applications of concepts and analogies can and should play in this. Because this issue is extensively addressed in the chapters in this volume (and elsewhere) we keep this discussion around SoK in science brief, and aim to only highlight points that are relevant for the following sections regarding SoK in cognition and education.

Scientific disciplines and philosophers of science vary in how they understand the structure of scientific theories. Overall, it appears that different disciplines or schools of thought differently value, strive for or consider achievable, *theoretical coherence* (across varying depths of explanation) and *scope* (across a breadth of phenomena) within their own field and in relation to other fields. Thagard (2007) argues that a theory that strives for “broadening coherence” (i.e. scope in terms of being able to explain more diverse phenomena) as well as “deepening coherence” (i.e. depth in terms of hypotheses being explained by more abstract theory) can be expected (but not guaranteed) to approximate (objective) truth the most based on what we know from the history of science and the structure of the world. Leaving aside such claims

about “objective truth”, others have suggested pragmatic reasons for striving for coherence in terms of depth and scope. For example, regarding sustainability science, Tavoni et al. (2014) highlight how disciplinary silos stifle progress in addressing sustainability challenges if they lead to incoherent predictions about the effects of interventions, and authors call for unification and coherence across ecology, economics, and behavioral sciences. The field of contextual behavioral science also starts from the truth criterion of pragmatism, meaning a theory is “true” if it works in relation to a goal - in the case of contextual behavioral science, the pragmatic aim is to predict and influence human behavior to towards valued living with (theoretical) precision, scope and depth (Hayes et al., 2012). Further pragmatic reasons for coherence from the point of view of learning and education will be addressed in the sections below.

Related to the structure of knowledge is also the discussion around the role and value of analogies in science. In this regard, Stanley (2020) proposes that some of the disagreements in evolutionary science about the validity and value of an analogy between biological evolution and cultural evolution, are based on misunderstandings about the analogical transfer of evolutionary concepts and processes: some scientists seem to think that an appropriate generalization of evolutionary processes depends on the degree to which these processes are similar to processes of genetic evolution. On this view, any divergence in cultural evolution from biological evolution is seen as a weakness of claims about the “evolutionary” aspects of culture. Stanley (2020) argues instead that the appropriate analogy is actually between the abstracted concepts (see table below) and the diversity of domains to which the concepts are applied. That is, in the example table below (adapted from Eirdosh & Hanisch 2021), we should not be directly concerned with the similarities between genetic, cognitive-behavioral, and cultural evolution, but rather, we should focus on how pragmatically valuable it may or may not be to apply the abstracted evolutionary concepts in understanding each of the domains on their own.

**Table 1:** Analogy table highlighting some possible domain-specific instantiations of abstract evolutionary concepts in genetic evolution, learning, and cultural evolution.

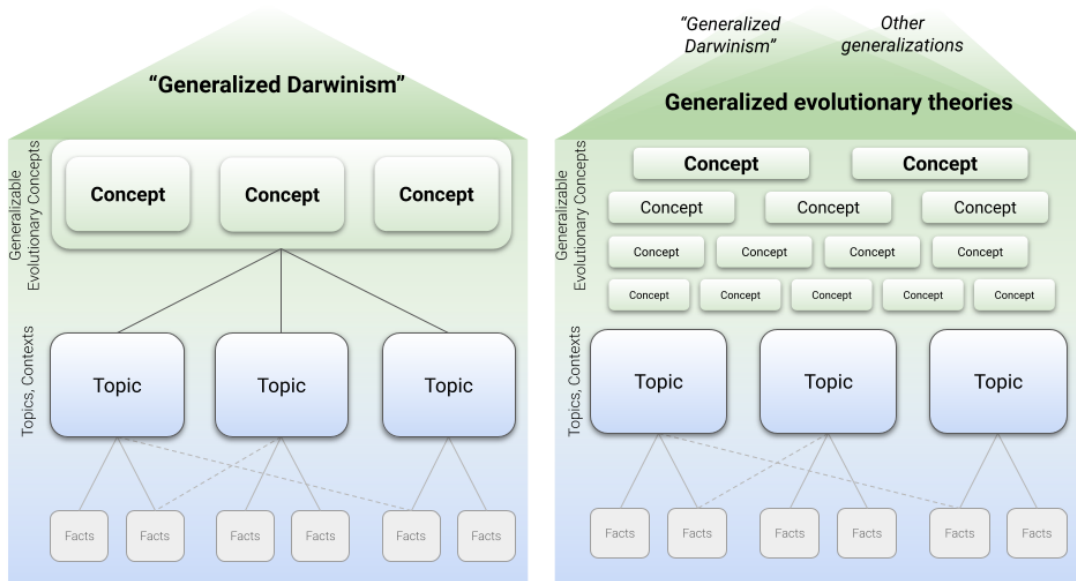
Abstracted Evolutionary Concepts	Domains		
	Genetic Evolution	Cognitive-Behavioral Evolution (Learning)	Cultural Evolution
How is <b>variation</b> of traits caused?	mutation, recombination	mistakes, recombination of prior learning, trial-and error learning, reactions to new environments, creativity, social learning	mistakes, recombination of ideas, trial-and error learning, reactions to new environments, creativity, between-group social learning
How does <b>selection</b> of traits occur	higher chances of survival and reproduction	selective attention, emotional strength, relation to prior learning, practical consequences	higher chances of survival and reproduction ( <i>natural selection</i> ); greater reward, appeal or attractiveness of the trait ( <i>cultural selection</i> )
How are traits <b>inherited, transmitted, or retained</b> ?	biological reproduction, mitosis/meiosis	encoding into long-term memory for later retrieval	social learning / imitation, teaching; technologies and infrastructure that endure

As Stanley describes:

*"... the ontologically minimalist process of evolution by natural selection can be realized by biological systems and by cultural systems, not because the two systems are alike, but because they both exhibit the relevant Darwinian properties of phenotypic variation, differential fitness, and heritability.*

*The mistake here, or, at least, the misleading move, is the apparent attempt to model the cultural evolutionary mechanisms as being in close correspondence with the biological evolutionary mechanisms. These mechanisms don't have to be similar, or analogous, or even to correspond in some one-to-one like manner; the mechanisms can be substantially different."*

As we build on Stanley’s critical distinction in analogical reasoning, we will also here point to an important difference in wording that is particularly relevant in discussing the teaching of generalized evolutionary thinking. Stanley frames his analysis in terms of “Darwinian” principles and theory, and provides his (reasonable in our view) framing of what “Darwinian” means in this discussion. We suggest that in the applied domain of evolution education, we can make greater progress by focusing on the challenges and opportunities of teaching about *generalizable evolutionary concepts*. As this volume documents, there is not currently, nor is there likely soon to emerge, a significant singular consensus on what “Generalized Darwinism” is. In spite of this lack of scientific agreement at that level of theoretical organization, there is virtually no disagreement that many of the individual concepts employed in evolutionary explanations (e.g. variation, inheritance, selection, function, fitness, adaptation etc.) can be, and routinely are, employed in contexts beyond genetic evolution. The boundaries of when an explanation that invokes evolutionary concepts becomes an evolutionary explanation, or the degree to which an evolutionary explanation can be said to be “Darwinian”, are fascinating and possible questions for classrooms to explore, but the existence of these questions are not arguments against the critical generalization of evolutionary concepts (fig. 2).



**Fig 2.** A structure of knowledge culminating in a specific body of theory (e.g. “Generalized Darwinism”) (left); and a more pluralistic structure of knowledge, allowing a complex landscape of generalized evolutionary theories to emerge from a range of evolutionary concepts and their relations.

A focus on the level of concepts and an openness regarding a specific target body of theory also relates to the aspect of pluralism that some scientists and philosophers of science call for.

For example, Lohse (this volume) is skeptical of attempts to use cultural evolutionary theory to synthesize the social sciences, highlighting that there may be several legitimate reasons for the pluralistic nature of the social sciences. Van Bouwel & Weber (2008) propose an explanatory pluralism that is based on the plurality of questions that can be asked about any phenomenon, as well as the plurality of goals or purposes that an explanation is meant to serve. Their approach is non-relativistic because given a question and a purpose, several explanations can still be compared and ranked by their accuracy, adequacy and efficiency. Similarly, addressing the debate about an extended evolutionary synthesis, Baedke et al. (2020) highlighted how different levels of evolutionary explanation can fulfill different explanatory standards, including precision and idealization/abstraction.

As we will show in the following sections, this debate in science around coherence, pragmatism, and pluralism is contextualized by views about human cognition and learning as well as by the goal of education of helping students develop a networked (i.e. coherent), multi- and interdisciplinary (i.e. pluralistic), and helpful (i.e. pragmatic) understanding of the world.

## Structures of knowledge in cognition

Psychology and cognitive science offer further insight into the role of structure of knowledge, concepts and analogies in learning and in relation to the potential of an interdisciplinary evolution education.

One example of this can be found in the field of psychology of science, which explores the psychological underpinnings of scientific reasoning, such as pattern recognition, categorization, association, causal reasoning, and analogical reasoning (Feist, 2006, 2013). Some developmental psychologists even make an analogy between the process of discovery and theory building in a scientific community and the process of learning during development (Gopnik et al., 1999; though the validity and usefulness of this analogy is also strongly debated, in some ways similarly to the debates surrounding the analogical nature of evolutionary concepts).

Regarding analogical reasoning, Gentner's structure mapping theory has been influential, which describes how learning and the build up of a structure of knowledge progress through analogical thinking:

*"The process of analogical thinking can be usefully decomposed into several basic constituent processes. In a typical reasoning scenario, one or more relevant analogs stored in long-term memory must be accessed. A familiar analog must be mapped to the target analog to identify systematic correspondences between the two, thereby aligning the corresponding parts of each analog. The resulting mapping allows analogical inferences to be made about the target analog,*



*thus creating new knowledge to fill gaps in understanding. These inferences need to be evaluated and possibly adapted to fit the unique requirements of the target. Finally, in the aftermath of analogical reasoning, learning can result in the generation of new categories and schemas, the addition of new instances to memory, and new understandings of old instances and schemas that allow them to be accessed better in the future.”* (Gentner et al. 2001 p. 9).

Generally, metaphor and analogy are considered to have central roles in human cognition and language. For example, Hofstadter (2001) proclaims that analogy is “the engine of cognition” and Lakoff & Johnson (1980) highlight how our everyday language is inherently metaphorical.

Of relevance for this discussion are suggestions regarding how humans tend to judge analogies to be “good”. For example, in the evaluation of analogies, studies show that factors like the degree of structural alignment; the amount of new knowledge that it generates; factual validity; adaptability of the relations to fit the target, and the relevance to current goals are influential (Gentner & Maravilla, 2018). Aspects of coherence as well as pragmatism and resulting pluralism are evident in these factors.

Regarding the degree of structural alignment, the systematicity principle has been proposed, which “reflects an implicit preference for coherence and predictive power in analogical processing” (Gentner & Colhoun, 2010, p. 37). Chesebrough et al. (2019) similarly highlight the role of coherence in efficient learning, stating that “Coherence exists when concepts “fit” together in ways that are unambiguous, consistent, and explicit. Content that is designed to optimize coherence creates vastly more effective learning.” and “Decoherence is created when the learner is unable to see clear connections, when the same concept is described in contradictory ways, or when the same language is used to describe different concepts”. This has clear implications for instructional design in evolution education, as will be highlighted below. Thus neural reward systems might indeed have evolved because of a higher adaptive value for coherence and generalizations in terms of scope and depth (Oh et al., 2020). This view has even led some cognitive scientists to speak of “explanation as orgasm” (Gopnik et al., 2001).

However, this doesn’t mean that human cognitive architecture always leads to optimized learning and approximation of objective “truth” (i.e. that humans are perfect Bayesian learners) or an entirely coherent structure of knowledge. This is partly due to various constraints, trade-offs, path-dependencies, and chance, just as in science and evolution. Furthermore, Legare & Shtulman (2018) highlight how humans seem to have coexisting domains of knowledge and pluralistic patterns of explanation which can be incoherent, such as both scientific and religious explanations, due to various sources of information and different kinds of goals as well as emotional aspects. Nonetheless, this does not mean that as educators, we can’t strive to help students develop a coherent structure of knowledge (see below) that helps

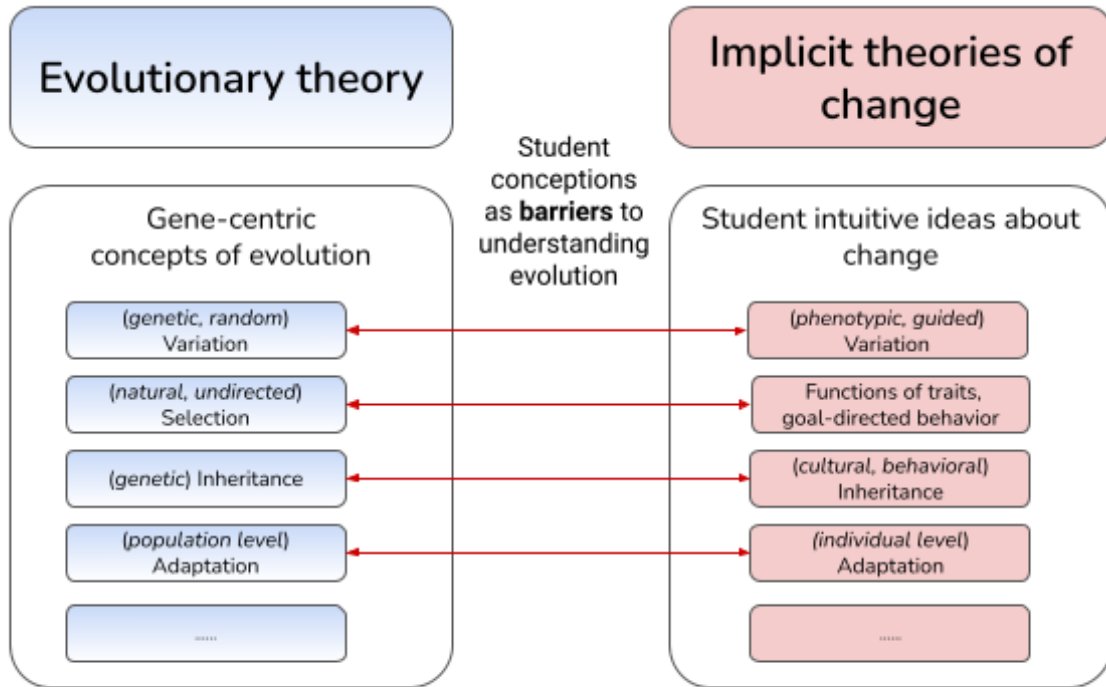
them to integrate, e.g. everyday experience and scientific theories. Indeed, Legare & Shtulman (2018) propose integrated reasoning as one way to resolve previously incoherent coexisting explanations. Thus, similar to the debates in science, human cognition appears to be structured towards a capacity for both creating coherence and enabling pluralism.

Another important element for understanding the role of structures of knowledge in cognition is the role of prior knowledge and its relationship to new information. Haskell (2000, p. 10) stated that “All learning involves transfer from prior learning to a greater or lesser degree”, and Chesebrough et al. (2019) explain that “information that is consistent with an individual’s existing schemas is more quickly mapped onto neural networks in the brain where that information is stored, whereas information that is inconsistent with prior schemas requires more energy and resources for the brain to integrate”.

With regard to teaching evolution, one can thus ask to what degree different formulations of evolutionary concepts and theory can productively relate to existing student mental models about their biological, social and psychological world. Different answers to these questions have been proposed and explored in the evolution education literature (fig. 3-5):

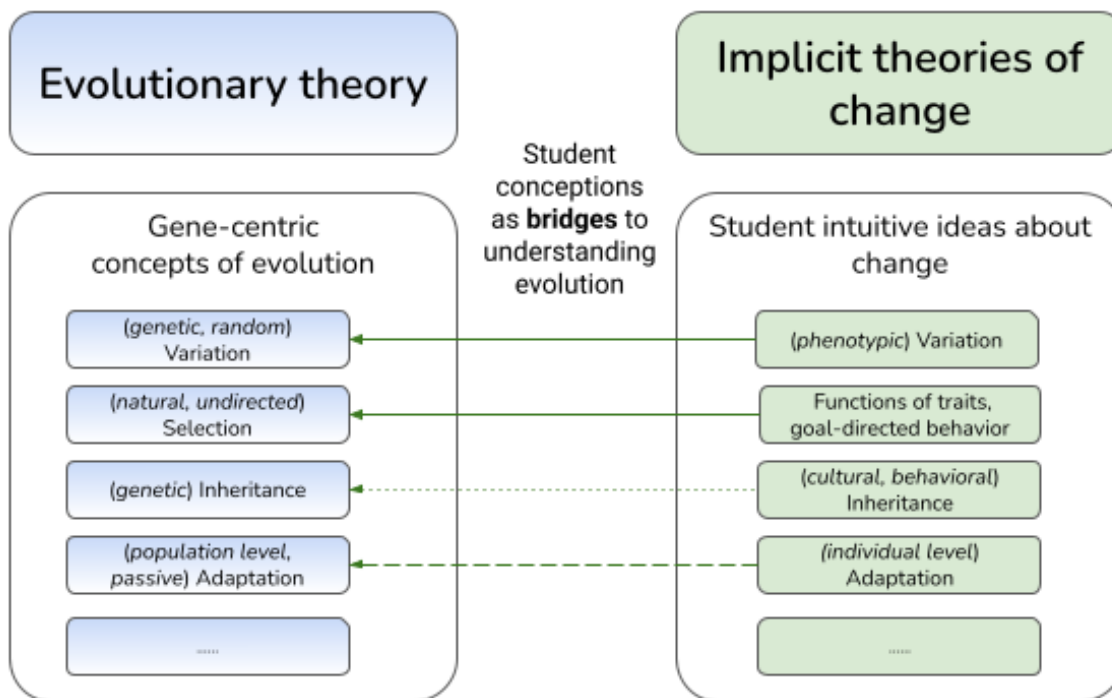
- Student intuitive conceptions/theories as barriers to understanding;
- Student intuitive conceptions/theories as bridges to understanding;
- Student intuitive conceptions/theories as foundations for understanding.

We argue that answers to these questions depend on the presumed structure of evolutionary theory and the presumed definitions and scope of evolutionary concepts.



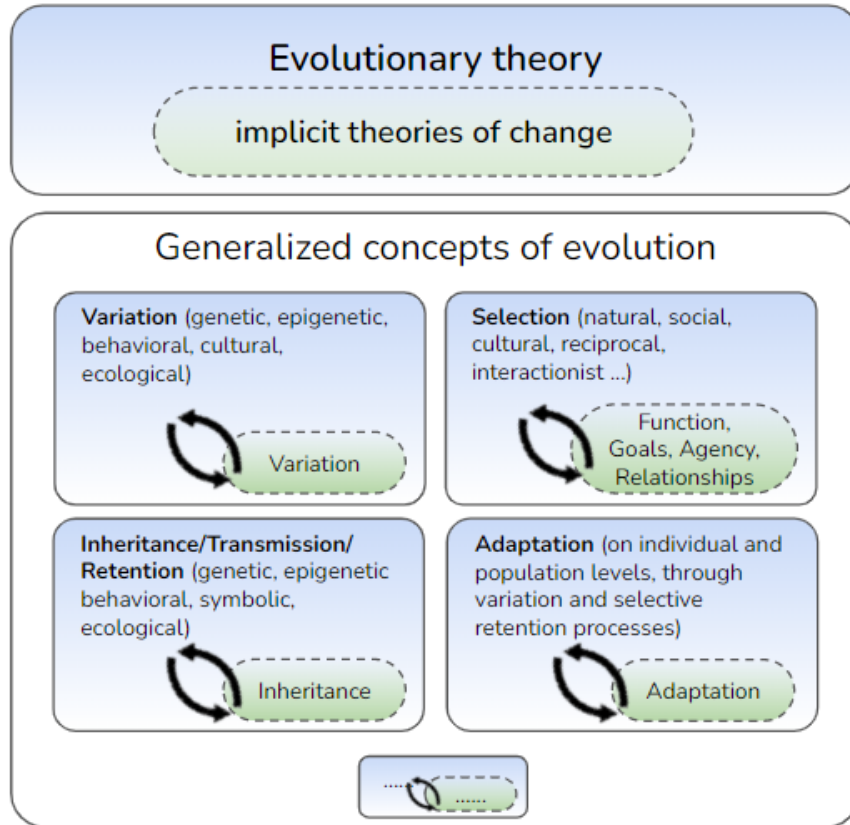
**Fig 3.** Student intuitive conceptions/theories as barriers to understanding

On the one hand, one can presume that evolutionary theory and students' intuitive theories are inherently at odds with each other, that they cannot be integrated coherently and that therefore student preconceptions present barriers to understanding evolution, or at least that they need to be left aside in the evolution education classroom (Fig. 3). We argue that this position makes sense if one presumes strictly gene-centric conceptualizations of evolutionary concepts, as well as if one presumes that organism agency and behavior have no role in evolutionary explanations (both of which are common assumptions in evolution education, see below). After all, students do not experience genes in their everyday lives, and students experience agency almost constantly.



**Fig 4.** Student intuitive conceptions/theories as bridges to understanding

Another view is that of students' intuitive theories of change as bridges to understanding evolutionary concepts (fig. 4). This is a view that has gained prevalence in education more generally, i.e. the idea that one cannot simply replace preconceptions with scientifically correct conceptions and that instead educators need to take preconceptions and prior knowledge as the only viable starting point for learning. In evolution education, students' intuitive understanding of function and needs has thus been regarded as a bridge or stepping stone towards understanding natural selection rather than a barrier (e.g. Bruckermann et al., 2020; Evans & Rosengren, 2018). Similarly, students' ability to see phenotypic variation is often used in evolution education in the early years as a starting point for understanding the role of variation in natural selection (see below). We are not aware of any studies in evolution education that explored students' intuitive understanding of (individual level) adaptation or of various inheritance streams (e.g. Moya et al., 2015) as bridges for understanding these evolutionary concepts, which is why in fig. 4, these aspects are presented as dotted lines. Importantly, most views of students' preconceptions as bridges towards understanding evolution still regard gene-centric and narrowly defined conceptualizations of evolutionary concepts as the "target", whereby student conceptions are merely stepping stones and are to be "left behind".



**Fig 5.** Student intuitive conceptions/theories as foundations for understanding

A third possible view regarding the relation of intuitive theories and evolutionary theory is presented in fig. 5. Here we argue that evolutionary theory and concepts can be integrated with students' prior concepts, that student conceptions provide viable foundations for understanding. This is afforded by generalized conceptualizations of evolutionary concepts and processes which include, e.g. aspects like social learning as an inheritance mechanism, or which allow variations and changes in technology, in musical styles, or in individual development and learning to be explored as evolutionary phenomena. These can be productively *integrated* with students' existing mental models, while gene-centric conceptualizations of evolutionary processes cannot. Importantly, in the process, student intuitive understandings can also be re-represented and complexified, making them coherent with scientifically sound conceptualizations, such as regarding the role of decentralized causation in cultural change. For example, in the service of complexifying student understanding about goal-directedness, we can help them see that their own behaviors are often not intentional, or do not entail explicit goals, or create unintended outcomes, in order to build a schema of decentralized causation that is connected to their everyday experience and that they can use to understand decentralized causation and goal-directedness in evolution. This approach is in contrast to the currently predominant approach in evolution education which regards goal-directedness as barriers to understanding (represented in fig. 3), but, we argue, one

that helps to build a conceptual coherence (scope and depth) and ultimately assists in deeper understanding.

Scientific reasoning is not just a purely rational process absent of emotional and motivational components. Cognitive scientists have also explored an affective and motivational dimension to analogical reasoning, in that certain analogies can elicit positive feelings, feelings of beauty and joy, enhance interest, inspiration or even self-confidence (e.g. Harrison, 2006; Thagard & Shelley, 2001). This aspect might have relevance to educational goals of fostering students' appreciation and motivation towards evolution, or enhancing attitudes like growth mindset and social-emotional learning. For example, in the field of contextual behavioral science, reinforcement learning is conceptualized as an evolutionary process (see table 1), and the self is conceptualized as a process, a context, a population or a system (Hayes et al., 2017). We would argue that such analogies present at least two sets of learning potentials to consider. One of them is that this schema of self as population, or self as complex system, instead of self as one fixed, essential entity, can be used to strengthen population thinking and a decentralized mindset (which should be of interest to the evolutionary biology educator). Additionally, the concept of the self as context or as process, instead of self as a fixed concept, relates to psychological flexibility (Kashdan & Rottenberg, 2010) and the learning goal of developing students' growth mindset (Dweck, 2012), i.e. the idea of the self as ever changing and able to improve through the ability for learning. In this way, by using generalizable evolutionary conceptualizations as the target of instructions, evolution education has the potential to build *both* understanding and emotional competency.

To conclude this section, besides the debate in science and philosophy, there are indications based on human cognition that tell us why we should indeed strive for coherence and encourage the flexible application of evolutionary concepts in developing students' structure of knowledge in (evolution) education.

## Structures of knowledge in education

In this section, we aim to highlight how the structure of knowledge that evolution education presumes with regard to evolutionary theory informs educational standards, assessment tools, and materials. We suggest that this presumed structure also creates incoherence with respect to the framing of concepts and with respect to the application of evolutionary concepts to phenomena in students' lives.

### Structure of knowledge and curriculum in evolution education

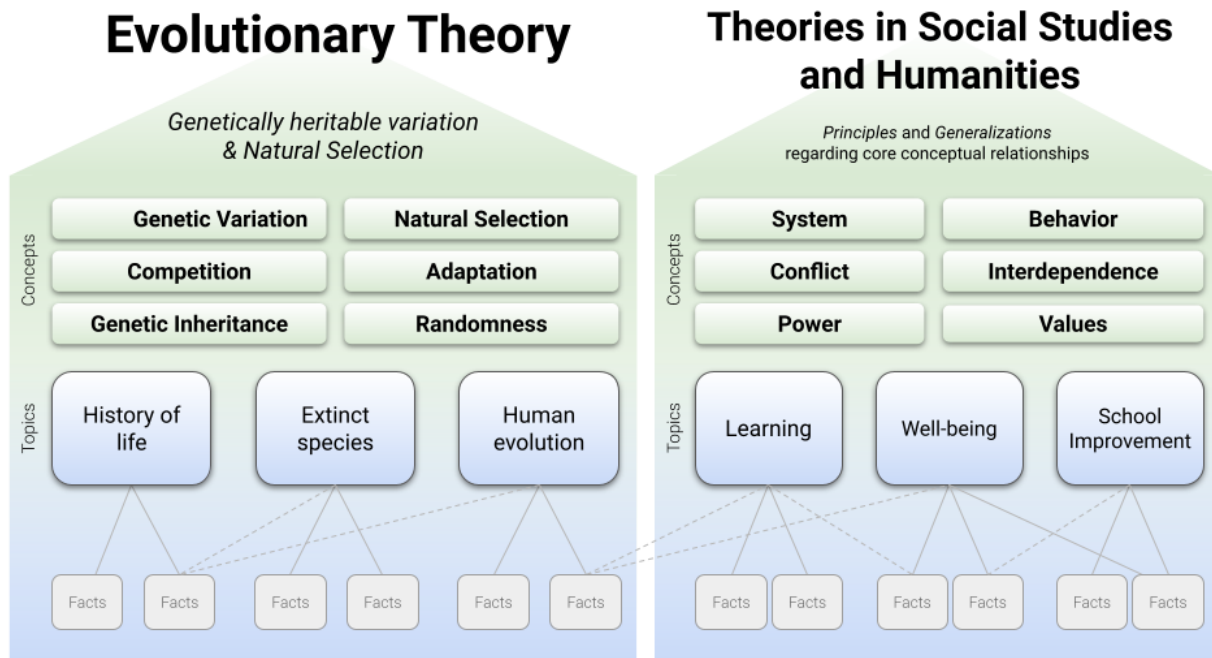
In education, perspectives around the structure of knowledge in science and cognition have strongly informed curriculum reform efforts since the end of the 20th century with the recognition that education needs to move away from coverage and rote learning of facts and

topics and towards developing a deeper and transferable structure of knowledge in students (Erickson et al., 2017). Additionally, given the cumulative nature of scientific knowledge about the world, education systems are increasingly faced with a challenge of “curriculum overload” that demands a focus on core ideas that are transferable to a wide diversity of phenomena across domains (OECD, 2020).

Standards and curricula have also at least partly supported a more interdisciplinary coherence. For example, in the US, the Next Generation Science Standards have been developed for the STEM (Science, Technology, Engineering, Mathematics) fields (NGSS Lead States, 2013a). The framework identifies “seven crosscutting concepts that bridge disciplinary boundaries, uniting core ideas throughout the fields of science and engineering. The purpose of this framework is to help students deepen their understanding of the disciplinary core ideas, and develop a coherent and scientifically based view of the world” (NGSS Lead States, 2013b, p. 1). These crosscutting concepts include pattern, cause and effect/mechanism and explanation, systems, structure and function, stability and change. Similarly, in Germany, the biology standards delineate the core concepts of system, structure, function, and (individual, evolutionary) development (KMK, 2004). Thus, the influence of complex systems science (see Box 1) is prevalent in the structure of these natural science standards.

While these developments are laudable, we wish to highlight an important point that is also indicative of wider patterns within the traditional structure of school curricula. That is, we are not aware of an overall structure or curriculum standard that spans social and natural science domains in education (fig. 6). This has implications for generalized evolutionary theory. One interesting case in point is the rather ambiguous place of (human) behavior in the curriculum. In the US, the NGSS specifically excluded behavioral and social sciences from its definition of “science education” (National Research Council, 2012). On the other hand, the US Social Science Standards do not integrate biological explanations of human behavior (National Council for the Social Studies, 2013). Some German states have also developed curriculum standards that integrate the STEM fields on the one hand, and that integrate the social studies fields on the other hand (e.g. Ministerium für Bildung, Wissenschaft, Weiterbildung und Kultur, 2014, 2016). Connections between (natural) science and social studies are encouraged, such as in the approach of socio-scientific issues (e.g. Zeidler et al., 2019), or within the NGSS in the core idea of science, technology and society, which prescribes that students explore “relationships among science, technology, and society”. (NGSS Lead States, 2013c). However, there does not appear to exist an overall structure of knowledge that integrates (human behavioral) concepts and theory across the natural sciences, social sciences and humanities, in current curriculum development. This ties into a much larger discussion about the role of social sciences or psychology within STEM education (e.g. Bray, 2010) as well as the philosophical possibilities and pitfalls of unification and synthesis across natural and social sciences (see also Lohse, this volume). The potential of generalized evolution to achieve at least partial theoretical coherence

between natural and social science, and even humanities (e.g. through digital humanities) is thus currently not yet explored in curriculum development. Overall, 21st century human sciences are fundamentally interdisciplinary, routinely crossing natural and social science boundaries, and currently this appears to not yet be sufficiently reflected in curriculum reform efforts.



**Fig 6.** Current structure of curriculum for many school systems around the world, with a distinct SoK for evolutionary concepts and theory which is largely, if not completely, separate from SoK in social studies and humanities.

Specific learning progressions have also been proposed for evolution education. These implicitly or explicitly build on a notion of structure of knowledge, by identifying core ideas or principles as strands that are revisited over a range of age or grade bands in order to achieve increasingly complex, networked, and abstract levels of understanding. For example, the Understanding Evolution conceptual framework (University of California Museum of Paleontology, 2009a) is an influential framework in evolution education that 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. Other learning progressions have been developed specifically for the younger years (K-6; Lehrer & Schauble, 2012; Russel & McGuigan, 2019).

These learning progressions cut evolutionary theory at somewhat different joints (sensu Plato), or start with different *optimal structures* (sensu Bruner, 1974) of evolutionary theory. For example, the learning progression of Lehrer & Schauble (2012) for K-6 years is structured around the constructs of change (in individuals and populations), variation, and ecosystems,



which they consider as "serving as a conceptual foundation for reasoning about the theory of evolution later in their education" (p. 701); whereas other learning progressions do not consider understandings of *individual* change as relevant to the theory of evolution. If anything they might consider them instead as misconceptions that present barriers to understanding, which highlights the different approaches shown in Fig. 3-5 above.

What also seems to happen in learning progressions is that in the younger grades, evolution education standards and learning progressions start with very general understandings of concepts like variation, information, trait, and then progress towards an increasingly gene-centric understanding of these concepts (rather than, e.g. retaining the general conceptualization and exploring their different applications across domains). For example, in the NGSS life science standards on the core idea of heredity, the understanding about variation in the primary grades is "Different organisms vary in how they look and function because they have different inherited information.", and in the following middle school grade levels, the general idea of information becomes constrained to genetic information, while in the high school grade levels, the role of environmental factors is again included, but it is not integrated or linked to the idea of inherited information (NGSS Lead States, 2013a).

We also observe other incoherent or changing use of concepts within standards and learning progressions. For example, the Understanding Evolution conceptual framework appears to reinforce a simple and direct genotype-phenotype relationship, or is at least not consistent about this relationship and its role in evolution. 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" (University of California Museum of Paleontology, 2009a). The framework also appears to be inconsistent regarding what levels of organization natural selection acts on. In the 12-16 grade level, we find the item "Natural selection is capable of acting at multiple hierarchical levels: on genes, on cells, on individuals, on populations, on species, and on larger clades." while in another instance, it is stated that "Populations, not individuals, evolve." (University of California Museum of Paleontology, 2009a). This is inconsistent or at least unclear, what is meant by "individual" and "population". 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? While experts in evolution science may be capable of interpreting the intended logic behind these statements, 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 coherence and understanding, especially for novice learners. Helping students to develop a generalized and transferable understanding of the population concept

(see Hanisch & Eirdosh, 2020b, for expanded discussion in evolution education; see Baragith, 2020, for a discussion in philosophy of biology) may help resolve this confusion.

Only at the 12-16 (post-secondary) grade levels is a definition of evolution offered in the Understanding Evolution framework, namely that “Evolution is often defined as a change in allele frequencies within a population.” (University of California Museum of Paleontology, 2009a). 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 different conceptualizations of evolution, including everyday conceptualizations.

## Structure of knowledge and instruction in evolution education

Looking at evolution education materials and assessment tools, we also find the clear influence of a gene-centric idealized formulation of evolutionary theory as well as instances of decoherence (*sensu* Cheseborough et al., 2019), unclarity and inconsistency regarding how to define and reason about evolutionary concepts. One might argue that the two are related - in that the gene-centric idealized formulation in fact leads to incoherence if it is applied to all phenomena uncritically.

A commonly used assessment tool is the Conceptual Inventory of Natural Selection (CINS; Anderson et al., 2002), which according to Mead et al. (2019) has been used in 31 publications from 1990-2016. It targets a number of concepts through a number of context examples, such as 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. 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. On the concept of heritable variation, a distractor item is “Traits acquired during an organism’s lifetime will be inherited by offspring”; and on the concept of change in a population, a distractor item is “Learned behaviors are inherited”. The problem is that 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 also often passed onto offspring in many species through the transmission mechanism of social learning (e.g. Hoppit & Laland, 2013; Jablonka & Lamb, 2005). This aspect is also something that students can be expected to have an intuitive understanding of based on their everyday experiences. Their reasoning (that learned behaviors can be inherited, or transmitted, to other organisms) might also be considered scientifically valid but such reasoning is not integrated productively into the educational practice but, in the case of this assessment item, rather thwarted.

Another prevalent assessment instrument is the Assessing COntextual Reasoning about Natural Selection (ACORNS, Nehm et al., 2012), which according to Mead et al. (2019) has been used in nine studies between 1990 and 2016. Among other things, it asks students “How would a biologist explain how [trait X] evolved?”, covering different context examples. We would argue that this question and the way that answers are analyzed reinforces notions that (a) all traits can be explained the same way, and (b) all biologists will explain a trait the same way. For example, student answers that say that they would need to know more about the function of a trait, are treated as misconceptions and receive a score of zero. It is quite astonishing that such a “blind”, even ritualized application of selectionist thinking across traits is put forward in such assessment and is considered an objective measure of “understanding”.

Overall, it appears that current assessment tools very often aim towards carving out and presenting an idealized structure of evolutionary theory (or sometimes targeting natural selection only) as if this is how biologists reason, generally and across contexts, about the evolution of traits, when in reality, the scientific discourse and practice is much more diverse and nuanced across the many biological and evolutionary subdisciplines. This relates to the debate around pluralism in science (see above). As Love (2013) points out, “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”.

A gene-centric structure of evolutionary theory has 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 individual-level 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, are not included in the unit purportedly asking “What does it mean to be human?”. Of course, it is possible to provide explanations only invoking mutations, morphology, and individual level competition and selection. To use the framework of van Bouwel & Weber (2008) - maybe such explanations can be considered the most *efficient*, but one can debate whether such explanations would be *adequate* for the purpose of asking the question “What does it mean to be human” in educational contexts.

Another example that illustrates how idealized concepts of evolution are implied to be adequate 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 mechanistic and central tenets of a gene-centric idealized model of evolution. 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 and cognitive-behavioral dynamics that are widely recognized as driving the evolution of our species.

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.” (University of California Museum of Paleontology, 2009a). Similar themes are pointed out by many other authors (e.g. Pobiner 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 (2020a), this may well have to do with the fact that many human traits do not have “simple” causes based on linear individual selection and genetics, meaning that they do not fit neatly into the idealized structure of evolutionary theory. They may even be considered as outside the realm of traditional STEM fields, and thus do not fit neatly into one of the traditional subject areas. Another application of evolutionary theory relevant to students’ everyday lives is the role of evolutionary algorithms in technology and artificial intelligence, but again, given the gene-centric formulations of evolutionary processes, such a link is also largely absent in educational discourse.

Another educational approach that has been proposed to increase student engagement in evolutionary theory is the reflection on how humans might continue to evolve in the present and in the future. For example, 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 increase in frequency 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).

Such classroom discussions may be more constructive for evolution education and enhance the development of a coherent structure of knowledge 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 these concepts fruitfully to issues of public health in human populations, which would allow students

to connect and reinforce their schema about evolutionary change. After all, possible trait transmission mechanisms other than genetic inheritance, such as social learning, 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 transferable fashion.

It is important to point out that we are not claiming that when exploring phenomena such as obesity, students should only be exposed to, or expected to generate, (generalized) *evolutionary* explanations, to the exclusion of other explanations, such as those that include other concepts from social sciences. As highlighted by van Bouwel & Weber (2008), “we should select the content of our explanation in such a way that it is adequate relative to our motivation for asking the question.” In this regard, van Bouwel & Weber (2008) also propose a “question-based pluralism”, meaning that “[f]or every social or historical phenomenon, there are many interesting and legitimate explanation-seeking questions that can be asked”, and hence different kinds of explanations can be considered adequate (or not adequate) depending on the question. In the case above, arguably the motivation for asking the question “Are humans evolving to become more obese?” was to see whether *evolutionary concepts* can play a role (and whether students can critically and adequately apply them) in explaining the observed phenomenon that the rate of obesity is increasing in society. Such focus on particular kinds of disciplinary concepts in a particular class is common educational practice and highlights that pluralism is somewhat baked into the curriculum. Clearly, in other subjects other concepts such as power, institutions, laws, norms, inequality, exercise, calorie, etc., may be equally applied to explore their role in explaining this particular phenomenon. When it comes to exploring *evolutionary concepts* in such phenomena, we argue that generalized (or generalizable) evolutionary concepts might make the discussion of such questions in the evolution education classroom more fruitful towards several learning goals, including in relation to providing conceptual coherence in evolutionary reasoning and increasing student motivation and interest.

Overall, despite the relevance of cultural evolutionary theory to students’ everyday lives and its potential to connect to various educational goals, there appears currently an inconsistent approach to integrating cultural evolution into evolution education. For example, the Understanding Evolution framework introduced above does not contain any cultural evolutionary notions of concepts. At the same time, the website features teaching materials about cultural evolution and linguistics (based on Thanukos, 2008), where it is stated that “in fact, evolutionary concepts can be applied even beyond the biological world. Any system that has variation, differential reproduction, and some form of inheritance will evolve if given enough time.” (University of California Museum of Paleontology, 2009b). A link is then made to the following conceptualizations in the framework: “Evolution results from selection acting upon *genetic*

variation within a population.” and “Evolution results from *genetic* drift acting upon *genetic* variation within a population” (emphases added). It is unclear how educators and learners should link the example content of the evolution of languages to the gene-centered conceptualizations put forward in the framework. Arguably the only ways to resolve this inconsistency is to either not include such examples as valid content for the evolution education classroom (thus forgoing opportunities for exploring evolutionary concepts across domains), or to amend the learning progressions to include more generalized conceptualizations of concepts.

At least in the German biology education context, the theme of cultural evolution appears in some state curricula (e.g. in the states of Saxony and Rhineland-Palatinate) and is covered in more or less depth in many 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, might choose answers on standardized evolution understanding assessment tools (see above) that would be evaluated as “wrong” from a gene-centric perspective, such as responses concerning the heritability of learned behaviors.

Critically, the latter textbook quoted above (Markl, 2018) 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 in the future of our species. That is, no supports are given for students to construct a coherent structure of knowledge in relation to the interdisciplinary application of evolutionary concepts.

To conclude this section, we find in the field of evolution education a mismatch between the educational goals that evolution educators aspire to (which include transferable understanding *as well as* emotional and motivational elements and competencies) on the one hand, and the structure of knowledge that is being reinforced through the conceptual and instructional tools that are employed on the other hand. The presumed gene-centric structure of knowledge that influences curriculum development and instructional design in evolution education might in fact hinder the field from achieving the full scope of their goals. Concurrently, we argue that the structure of knowledge (including its pluralistic nature) that is emerging from the current scientific discourse around generalizing evolutionary concepts and theory, may serve as a promising direction to address these issues.

## Curriculum and instructional design implications of a generalized evolutionary theory

If we take seriously the goals of 21st century education regarding the development of deep and transferable understandings, and the role of structures of knowledge in science and cognition, we see a great potential of, even a need for, integrating interdisciplinary evolutionary sciences in evolution education.

In fact, an excursion to the field of complex systems science and its influence on curriculum design and instruction (Box 1), hints at the opportunities that the evolution education community could engage in.

In the following sections, we propose steps to enable the teaching of evolutionary concepts as generalizable concepts to be applied critically across disciplines beyond biology, similar to concepts of complex systems dynamics:

- Learning progressions need to be re-examined and re-designed with an emphasis on the development of transferable conceptual understandings of core evolutionary concepts across disciplinary contexts.
- Evolution education should more strongly embrace instructional methods of teaching for conceptual understanding and transfer of learning, and accordingly re-negotiate targeted learning outcomes and methods for their assessment.
- Evolutionary thinking can and should be seen and treated as a subset of (or overlapping with) systems thinking, and pedagogical practices aimed at teaching for a transferable conceptual understanding of systems science concepts should also be more strongly integrated in evolution education towards understanding evolution science across disciplines.



### **Box: Excursion - Comparing complex systems science and evolution science in curriculum design**

Complex systems science explores dynamics of systems across domains which are characterized by many interacting elements, and exhibit decentralized causality, nonlinearity, feedback loops, and emergence. This body of theory and methods was greatly advanced through developments in mathematics and computer science since the 1970's and now informs disciplines like earth science, economics, and biology (Gleick, 1987). In a recent example of this influence, Jamie Davies has used a complex systems view of developmental biology to propose that, while the DNA double helix has become *the* icon of biology in the 20th century, a better icon for biology in the 21st century is the feedback loop: "The helix is too well-established an icon to be deposed any time soon. And yet, a simple loop would be a much more universal symbol of how life works at all of its scales and levels." (Davies, 2014). This sentiment reflects a broader shift in the biological sciences towards the application of generalized systems concepts, as in systems biology (e.g. Noble, 2006), behavioral biology (e.g. Sapolsky, 2018), and recent approaches in genomics (Gregory et al., 2016).

Concurrently with these developments in scientific theory and practice, complex systems science has also informed the teaching of many different subject areas, and current curriculum standards increasingly recognize the need to develop systems thinking competencies in students. As a result, many education fields readily recognize that the science and understanding of systems dynamics can be applied to a wide range of phenomena. A whole area of educational science explores the educational practice and assessment for developing students' understanding of complex systems, beginning in the primary school years (e.g. Booth Sweeney, 2006; Booth Sweeney & Sterman, 2007; Grotzer et al., 2017; Jacobson & Wilensky, 2006).

One might think that the generalization of evolutionary theory and of evolutionary concepts and processes to different domains would be similarly welcome by the education community. After all, evolutionary processes can be understood as a subset of complex systems processes, especially relevant to complex *adaptive* systems (see also Schurz in this volume). However, compared with systems science concepts, evolutionary concepts are not as commonly viewed in terms of interdisciplinary curriculum structures.

We propose that this difference in development may be for reasons that have to do with the different history and sociology of science that evolutionary theory has compared to complex systems science.

Despite the fact that evolutionary thinking has a long history across disciplines (see e.g. Veblen, 1898), the rise of the Modern Synthesis (MS) in the 1940's, which integrated insights of genetics and microbiology, advanced a popular view that evolutionary theory is properly understood as the purview of the biological domain, and by extension, the biology curriculum and classroom. In terms of complex systems science, however, the origin is rather in math, physics and computer science which dealt with complex systems dynamics in a much more abstract, domain-general fashion from the beginning (Gleick, 1987). Thus, developments in

interdisciplinary evolutionary theory have different implications for biologists because, historically, teaching evolution has been the task of biology educators, who have learned a biology-centric conceptualisation of evolution, largely informed by the MS, and have developed curriculum standards, instructional methods and materials as well as assessment tools and research programs that target those conceptions.

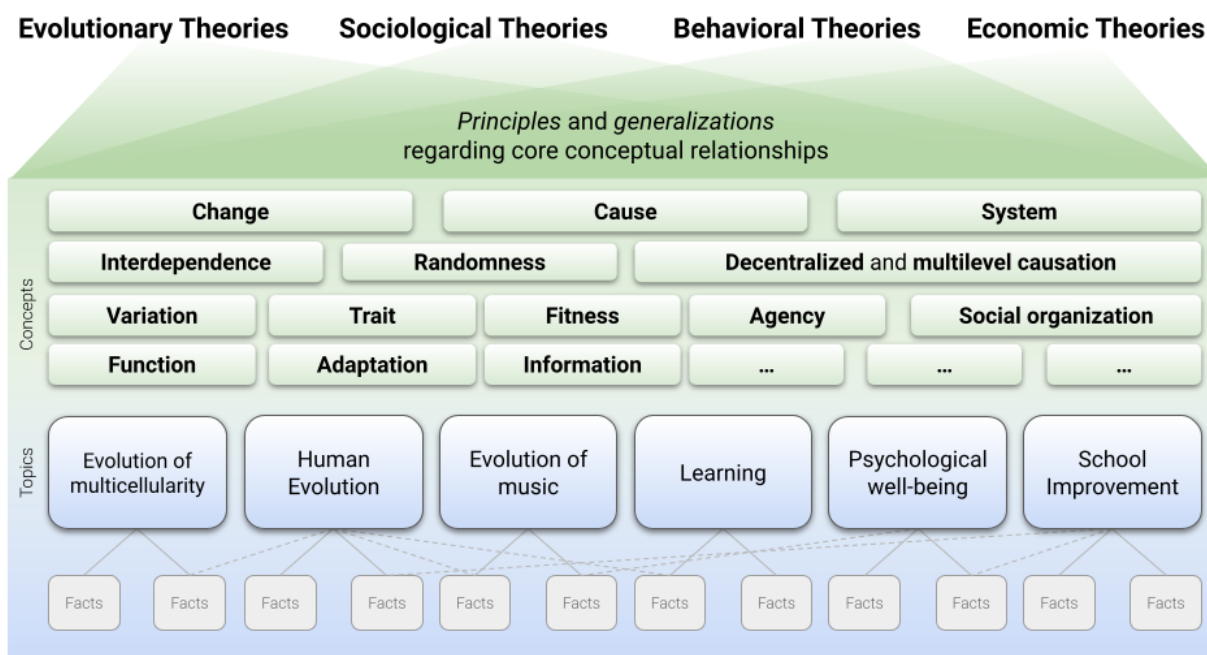
Another complication of generalizing evolutionary theory in educational contexts, compared to complex systems science, is that evolution entails both microevolutionary processes of change, and macroevolutionary patterns of the history of life on earth, including age of life on earth and common descent of all species. Thus, in contrast to systems science, evolutionary theory also attempts to explain the origins of today's observable organisms and their traits, including human traits, with the help of the combination of microevolutionary and macroevolutionary components, and this has strong implications for our worldviews, values, politics, and understandings of our place in the world, and thus has a complex relation to normative claims. Thus, integrating generalized conceptual understanding of evolutionary processes into the curriculum may be conceptually more complex in some dimensions. However, this may not mean it is actually more complex to teach or learn in practice. This added complexity may in fact be viewed as a pedagogical opportunity rather than challenge.

Finally, evolutionary theory comes with much more political and moral baggage due to its history, compared to complex systems science, because evolutionary theory was advanced at a time when the socio-political landscape, together with the (comparatively low) level of knowledge about human diversity and its origins, lead to wrong inferences to the social domain, including eugenic notions. Eugenics being a field which many historical evolutionary scientists, including Darwin, Haeckel and Julian Huxley, can, from today's standpoint, be seen as engaging in an ethically questionable or unacceptable fashion (e.g. Fuentes, 2021, and responses to him). The notion of social darwinism implied that using evolutionary theory to explain human cognition and culture is tantamount to eugenics. Thus, educational systems in the second half of the 20th century effectively constrained evolutionary thinking to biology, and a whole generation of educators, in biology and other subjects, seems to have been trained to be wary of any application of evolution to the human domain, particularly human cognition and culture.

In summary, the potential and limits of generalizability of concepts in complex systems and evolutionary sciences seem to be similar if not identical, yet the role of these concepts in general education curricula has developed along two very different trajectories. This seems to have more to do with the different history and sociology of these two fields of science rather than their conceptual structure. We suggest curriculum designers and interdisciplinary scientific teams work together to rethink the potential of correcting these trends towards engaging students in the critical application of generalized evolutionary concepts.

## Learning progressions and curriculum design

Current evolution learning progressions and standards are largely designed from a gene-centric (MS) structure of evolutionary theory. While this may have been functional in the past because evolutionary theory has been dominantly situated in the biological domain, we find that the various generalizations of evolutionary theory within current scientific work (as well as the inherently metaphorical nature of evolutionary concepts such that we find them in everyday language) demand new frameworks that explicitly incorporate more generalized notions of evolutionary concepts and processes within biology (see e.g. Araújo, 2020) as well as across the general education curriculum (Fig. 7).



**Fig. 7:** Possible structure of curriculum with the role of evolutionary concepts (besides other disciplinary concepts) across natural and social science theories.

Above we highlighted how, in current learning progressions, understandings in early years tend to start with generalizable conceptions (e.g. Lehrer & Schauble, 2012; University of California Museum of Paleontology, 2009a), while in later years these conceptualizations become increasingly gene-centric. We propose that learning progressions can instead focus on the generalizability of concepts and principles and their context- or domain-specific conceptualizations throughout. Evolution education can renegotiate its scope in the curriculum, and go beyond gene-centric notions, allowing connections to be made to a wider range of phenomena that include culture, psychology, and technology (fig. 7).

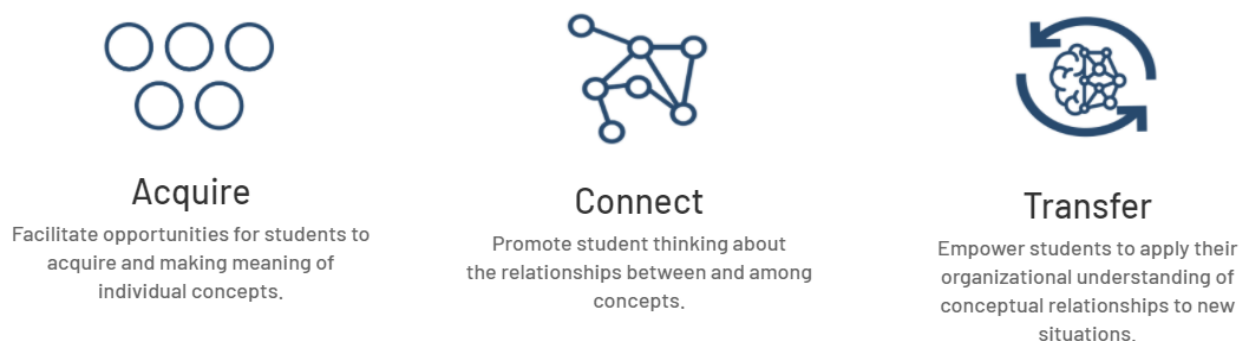
However, this requires a more coordinated effort across traditional domains in education systems, especially across the natural and social sciences. Biology educators might object that they do not need to concern themselves with a generalized evolutionary theory, such as cultural evolution, in their teaching of evolutionary concepts. We argue that this stance invites incoherence in the curriculum and in student cognition and results in inefficient learning of evolutionary concepts. Scientific developments like cultural evolution have already entered into the curriculum (see examples above), but under the currently prevalent framings of evolutionary theory in standards, assessment tools and materials, this increasingly creates incoherence and confusion. A coordinated approach to curriculum development that spans the natural and social sciences would offer a great new frontier for coherence, expanding on the curriculum reform movements that aim to strengthen interdisciplinary connections.

## Teaching for conceptual understanding and transfer of learning

Informed by cognitive science and the structure of knowledge, many educators highlight the role of teaching for conceptual understanding, analogical reasoning, and transfer of learning in order to develop deeper structures of knowledge and enable students to use their understandings in novel contexts.

We argue that the diverse generalizations and applications of evolutionary concepts in science as well as the philosophy of science discussions around these developments, provide great opportunity for a renewed emphasis on teaching for conceptual understanding and transfer of learning in evolution education. In this regard, Reydon (2020) criticized the conceptual change literature for assuming that there are correct and consensus understandings of scientific concepts that are the target of instruction, including in evolutionary science. He highlights how scientists often or usually use different conceptualizations of a concept, and that conceptualizations change over time. As the debate around a generalization of evolutionary theory shows, there is no singularly true “consensus” view on what concepts of evolutionary theory mean and to which phenomena they can be applied, and thus any particular understanding of a concept (Reydon uses the example of fitness), should not be the target of instruction. Instead, he argues that educational practice should help students in engaging in a whole space of how a particular concept can be understood and conceptualized by exploring the history of science, their own everyday conceptions, or conceptions of scientists studying different phenomena. In this regard, it is interesting that evolution educators and learning progressions often highlight and include the role of teaching the Nature of Science as part of fostering evolution understanding (e.g. Nelson et al., 2019; University of California Museum of Paleontology, 2009a). However, while Nature of Science is usually thought to include this view implicitly, it does not seem to include teaching about the *nature of concepts* and *conceptions* as part of nature of science and scientific discourse explicitly (see e.g. Lederman et al., 2002).

Erickson et al. (2017) and Stern et al. (2017, 2021) propose a range of approaches to focus curriculum and instructional design on developing such understandings of concepts and generalizations. The learning transfer method proposed by Stern et al. (2021; fig. 8) targets conceptual understanding, including the metacognitive understanding of concepts themselves. It starts by helping students attain understandings of certain core concepts of a field by exploring what they know about the concept, finding examples and nonexamples, identifying attributes and constructing their own definitions. Over time and by exploring further examples of a concept, students also deepen and complexify their understanding. As a next step, teachers help students explore how concepts relate to each other to form generalizations and principles by investigating specific phenomena where these relationships can be “uncovered”. Finally, teachers help students transfer their understandings by exploring how those generalizations and principles apply (or don’t apply) across various phenomena, in the process further complexifying their thinking.



**Fig. 8** The basic process of teaching for transfer (Image source: based on Stern et al., 2021, p. 10).

A large body of literature also focuses on instructional methods for the use of models, case comparisons, and analogies for targeting transfer of learning (e.g. Alfieri et al., 2013; Haskell, 2000; Harrison & Treagust, 2000; Vendetti et al., 2015). The instructional method of analogy mapping guides students in comparing phenomena by underlying principles or concepts, as well as differences between them, enabling them to look beyond surface features and achieve a more abstract representation (see table 1; Glynn, 2008). Interestingly, far analogies (that are more different in surface features) have been shown to lead to deeper learning than near analogies (Walker et al., 2018).

With such tools, we can help students re-represent and complexify their existing mental models about change, in order to make them coherent with evolutionary and decentralized, complex change (see Fig. 5). We would first help students unpack, complexify, explain, and relate the existing conceptualizations they might have in their mind about particular concepts such as “adaptation” or “development” or “learning”, to construct a definition of these terms, to find

examples and non-examples of these concepts, or to create a causal diagram linking environment, organism behaviors, other traits, genes etc. (see Hanisch & Eirdosh 2020c). As students then explore adaptation on phylogenetic time scales, we do not throw out their existing mental models about the concepts, but we would encourage them to compare the two - how are they similar, how are they different, how does understanding one of them help us in understanding the other, or how does understanding one change and enhance our understanding of the other, how does comparing both lead to a more abstract, transferable schema about the nature of change by evolutionary processes?

Students can even be offered conceptual questions such as “How is evolution like individual development, how is it different?” or “How is evolution like learning, how is it different?”, or “How is the evolution of species like the evolution of [cultural trait X], how is it different?” as an anchor question that is revisited throughout a unit on evolution (see e.g. Pugh et al., 2014). Such explorations can be adapted for different ages or classroom contexts.

A focus on conceptual understanding also calls for new approaches to assessment. Stern et al. (2017, 2021) propose assessment tools including self-and peer-assessment that encourage students to reflect on their changing conceptualizations and apply them critically to new and increasingly different phenomena. One can conceive of final assessment tasks in which students are presented with a phenomenon of trait change in the world, such as the spread of a new virus variant, or of anti-vaccine sentiments, the adoption of a technology, or changes of the distribution or characteristics of species and ecosystems in response to climate change, and to use their understanding of evolutionary concepts and processes to explain these phenomena and even develop or reflect on potential interventions. This would be quite similar to the question “How would a biologist explain...” as used in one evolution assessment tool (Nehm et al., 2012; see above), but reframed more generally as “How would an evolutionary scientist explain ...”, and it would look for students to ask the right questions and look for the right evidence in relation to the phenomenon, rather than for a rigid application of words and concepts. On the other hand, educators often still need efficient and standardized assessment tools such as multiple choice tests. Such assessment tools that are currently in use need to be reexamined critically to assure that they do not contain “trick questions” that leave space for interpretation (especially regarding the different possible conceptualizations of evolutionary concepts), are not merely testing for the ritualized learning of “how to pass the test” or “what the teacher wants to hear” and do not negatively assess students whose thinking can in fact be considered scientifically valid.

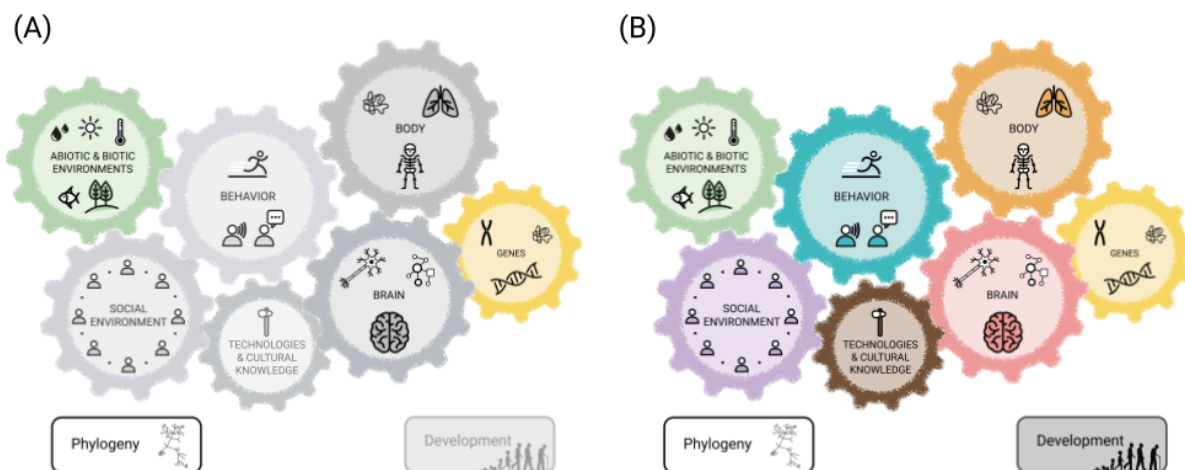
## Integrate and foster systems thinking in evolution education

As we have argued in Box 1, the teaching of evolution as a generalized and interdisciplinary science can be informed by the success of teaching about domain-general complex systems

dynamics, even at primary and middle school levels. Various teaching tools such as causal maps (Hanisch & Eirdosh, 2020c) and computer simulations (e.g. Centola et al., 2000) are available to teach students the complex nature of evolutionary change, from the start, with relatively simple models. For example, Roberts (1978) showed that middle school students could be taught to understand complex systems dynamics on a level comparable to MIT undergraduate courses with the help of scaffolded causal diagrams and explanation prompts. Thus, from a pedagogical view, it is important to emphasise that leading with complexity in the evolution classroom does not need to be “too complex” for students at certain grade levels given the right teaching methods.

We argue that evolution education can and should more strongly integrate such instruction and assessment methods of complex systems education into the evolution educators’ toolkit. For example, causal diagrams as used in complex systems education can be modified to include mechanisms and causal factors that are considered relevant in the evolution (and development) of particular traits, populations or systems of interest. In Hanisch & Eirdosh (2020c) we propose such a causal mapping toolkit for evolution education that allows the integration of development and evolution, of a range of causal factors (including behavior, culture, social environment as well as genes) and processes, complex systems dynamics such as feedback loops and decentralized causality.

We can also use instructional tools that reduce complexity by providing scaffolded representations and examples that chunk complexity *at the right joints*, or sequence it appropriately. In this way, specific causal relationships between factors and causal mechanisms can be introduced sequentially, e.g. by exploring relevant phenomena that help students uncover those relationships. The individual-level, unidirectional natural selection of morphological traits that have relatively direct genotype-phenotype relationship is *just one* of those phenomena that can be explored (Fig. 9a). However, importantly, we argue that evolution education should not stop there. More complex traits such as behavioral traits that include the important role of learning or of the social environment, can equally be explored and visualized, so long as they are integrated into an overall coherent structure of knowledge, rather than treated as “a new topic” (Fig. 9b). Diverse sources of facts, including genetics and archeology, but also examples from developmental, cross-species, cross-cultural behavioral and social science research can help to illustrate and uncover those relationships. Students can and should be challenged to articulate and defend their causal models on the basis of accessible information.



**Fig. 9.** A possible “cutting at the joints” of complex causal relationships in the evolution and development of developmental systems. (A) Emphasis on unidirectional natural selection of genetic variants by a particular environment over phylogeny, while backgrounding other factors and causal relationships, which is helpful when exploring particular evolutionary phenomena; (B) Expansion of the model by adding further traits and factors, thus building a more complete mental model of the causal relationships that need to be considered in explanations of the evolution and development of traits and developmental systems.

## Conclusions: Evolving an interdisciplinary evolution education?

Lewontin (1974) said, “to concentrate only on genetic change, without attempting to relate it to the kinds of physiological, morphogenetic, and behavioral evolution that are manifest in the fossil record, is to forget entirely what it is we are trying to explain in the first place”. (p. 23).

We argue that in a similar vein, to concentrate only on the formulation of evolutionary theory of the MS in evolution education is to forget entirely what it is we are trying to achieve in evolution education and education in the broadest sense. In light of the successful applications of evolutionary concepts and methods across disciplines as diverse as economics, anthropology, history, psychology, and computer science, gene-centered evolution education is increasingly climbing the wrong mountain (*sensu* Hanisch & Eirodsh, 2020a). Given the urgency of evolving adaptive learning environments for all humans on the planet, we suggest evolution education specialists and interdisciplinary education innovators and policy makers work together to advance a new vision regarding the role of evolutionary concepts in the general education curriculum.



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