Teaching **Evolution** as an **Interdisciplinary** Science

Concepts, Theory, and Network Infrastructure for Educational Design Research

Doctoral Thesis
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Submitted, October 2021

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Comparative Cultural Psychology

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Concepts, Theory, and Network Infrastructure
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Cumulative Dissertation

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Acknowledgments

Since before the start of my doctoral work, I have claimed that teaching about the evolution of cooperation will itself require the evolution of new networks of cooperation, across disciplines, sectors, and generations. The existence of this thesis is a testament to the early emergence of these networks. So many individuals, organizations, and institutions have contributed to my success, the following is an attempt to express my gratitude to some of the closest collaborators.

Guidance for thesis acknowledgements suggest I move from the more professional to the more personal. When one's most vital collaborator is also one's wife, this distinction becomes impossible. Susan Hanisch (Susi) is both the love of my life and the most brilliant and passionate colleague a researcher could hope for. She will often credit (or blame) me for enticing her away from the disciplinary bounds of agricultural sciences and into the complexities of evolution education, yet it is her relentless drive and organization that has pushed our original vision to our current heights. We have perhaps flown too close to the sun, but I believe our wings are not burned beyond repair.

Following this, I must share my deepest thanks to the constellation of innovation that makes up the Max Planck Society and the Max Planck Institute for Evolutionary Anthropology (MPI-EVA). Daniel Haun has been a key supporter of this work since he agreed to be my secondary supervisor in 2016. However, prior to my arrival in Daniel's newly minted Department of Comparative Cultural Psychology in May 2019, I was two years into my thesis with a very dim view on my prospects for success. Daniel made it clear from the beginning of my time at MPI-EVA that my eccentricities and transdisciplinarity were no longer liabilities, but assets to be refined within the incubating confines of our unique scientific culture. Daniel's secret to success is also cooperation, and so it is that our amazing departmental team and extended networks have also supported the core of this work. Anja Reimann, Isabella Eber, Katharina Haberl, Susanne Mauritz, Jana Jurkat, Petra Jahn, Daniel Hanus, Hanna Petschauer, and the entire the Wolfgang Köhler Primate Research Center team all provided a welcome new home and supports in setting up our educational work within the department. Ronny Barr and the MPI-EVA Media department have worked closely with us on developing the graphic design concepts and resources for our educational ecosystem. Steven Kalinke has fielded endless IT questions in the development of OpenEvo. Former MPI-EVA researchers, Esther Herrmann and Rebecca Koomen offered critical collaboration on teaching about their research. Student assistants Peter Hammel and Moritz Schmid have also contributed both through lab work and reflective discussions.

I was also incredibly fortunate to grow a cooperation with my thesis supervisor, Uwe Hossfeld, and his Biology Education working group at the University of Jena. Uwe's group in the BienenHaus (Bee House) of the Jena Campus is doing something unique within a field of biology education in need of innovators. It is an honor to be finalizing my work here and continuing our discussions into the future.

The beautiful city of Leipzig has also been the home to many other collaborators. Axel Kästner opened his Zoo School to us for extensive observations and pedagogical discussions. At the University of Leipzig, the Zentrum für Lehrerbildung und Schulforschung (ZLS, Center for Teacher Education and School Research) has been an invaluable partner in developing our teacher education module. Chris Bayer from Ancient Ancestors provided not only a collection of hominid fossil replicas for our Community Science Lab, but also a world of innovation in human evolution education. Educators Silke Duden and Silke Höfer opened their classrooms to our model, allowing this great experiment to gain real world traction.

Critically, a core of my collaborators in this work are on their own formal learning journey as well. The founding youth members of our Community Science Lab, Sanna Garrett, Vincent Voitel, Finn Pfeifer, and Jakob Sachse entered our institute at the end of 7th grade, and they still have not left, now at the start of their 10th grade year. I regard them as authentic collaborators in the development of our Community Science Lab model, and at this task they excel in both skill and spirit. That students can help drive the cultural evolution of schools should give us all some added hope for our troubled world.

At the global level, the entire Prosocial Schools team and Prosocial World community, particularly Peter Bullock, Paul Atkins, and David Sloan Wilson, have all been inspirational supporters and collaborators in evolving our vision for a learning planet. David in particular has been incredibly generous with his time and support over our last decade of exchanges and collaborations. Also from our broader network within the Association for Contextual Behavioral Sciences, Lauren Porosoff and Jonathan Weinstein provided wisdom and invaluable tools at critical moments during some of our earliest rough spots in this work.

Lastly, to my parents, John and Roseanna. Many have predicted over my childhood and life that I would not be able to make this work. You never questioned that I would, and never suggested that I shouldn't try, even when that path has led me well beyond the edges of normalcy. No child could ask for more than two parents that have helped them to pursue their dreams as much as you have helped me.

Keywords: Evolution education, Education for Sustainable Development (ESD), human behavioral, cognitive, and cultural evolution, interdisciplinary education

Abstract:

Evolution is an interdisciplinary science. Evolutionary theory is routinely employed across the overlapping domains of the natural, social, and computational sciences, as a high level generalization of processes of change within complex adaptive systems. Despite this interdisciplinary character of evolutionary science, evolution education remains almost exclusively the purview of the biology classroom within general education curricula around the world. This thesis engages conceptual clarification and educational design research to map and explore the educational potential of teaching evolution as the interdisciplinary science that it is. Beginning with a foray into student conceptions of the capacities for and causes of cooperation in chimpanzees and human children, it is argued that research in comparative psychology provides a fertile entry point for engaging the interdisciplinarity of evolutionary sciences. A considered analysis of persistent challenges within traditional approaches to biological evolution education then outlines core conceptual issues and pedagogical strategies for an interdisciplinary approach. This conceptual work supports the exploratory development of two novel directions in evolution education. First, in human evolution, a new toolkit is presented to engage students in causal mapping of the many processes and information streams that have shaped human origins. Second, an interdisciplinary approach to community-based school improvement has been developed that empowers youth to become drivers of valued change within their school community, while challenging them to reflect on the evolutionary theoretical context for such cultural change. Future directions in research are discussed within the context of the OpenEvo learning hub, an online educational innovation and design research lab to drive continued development in this space. Conclusions highlight the expansive potential and need for cooperation across the science-to-learning chain if we are to leverage the educational potential of this 21st century scientific synthesis.

Zusammenfassung:

Die Evolutionswissenschaften sind ein interdisziplinäres Feld, denn die Evolutionstheorie wird zunehmend sowohl in den Naturwissenschaften und der Informatik als auch in den Sozial- und Geisteswissenschaften als eine Grundlage für das Erforschen von Veränderungsprozessen in komplexen adaptiven Systemen gesehen. Trotz diesem interdisziplinären Character der Evolutionswissenschaften ist der Evolutionsunterricht nach wie vor fast ausschließlich im Fach Biologie und dessen Lehrplänen zu finden. Diese Dissertation beschäftigt sich damit, mithilfe von fachlicher Klärung und design-basierter Forschung das Bildungspotential eines interdisziplinären Evolutionsunterrichts zu beleuchten. Zunächst werden die im Rahmen einer Studie erhobenen Vorstellungen von SchülerInnen und Studierenden zu den Fähigkeiten und Ursachen von Kooperation von Menschen und Schimpansen vorgestellt, und es wird herausgestellt, dass die vergleichende Psychologie fruchtbare Inhalte für die Behandlung einer stärker interdisziplinär ausgerichteten Evolutionsforschung im Unterricht bietet. In einem weiteren Beitrag werden die anhaltenden Herausforderungen bezüglich dem Verständnis und der Akzeptanz der Evolutionstheorie im Rahmen des traditionellen biologischen Evolutionsunterrichts analysiert und daran anknüpfende Potenziale und Strategien eines interdisziplinären Evolutionsunterrichts identifiziert. Zwei konkrete Beispiele für die Unterrichtspraxis werden im Anschluss vorgestellt. Zum einen wird aufgezeigt, dass Ursache-Wirkungs-Diagramme innovative Lehr-/Lernmittel für den Evolutionsunterricht darstellen, welche es erlauben, mehrere Prozesse und Informationsströme in der Evolution und Entwicklung menschlicher Merkmale abzubilden. Zum anderen wird der Ansatz der *community-based* Schulentwicklung vorgestellt, welcher SchülerInnen befähigt, an wertorientierten Änderungsprozessen ihrer Schule mitzuwirken, und gleichzeitig über die theoretischen evolutionären Grundlagen dieser kulturellen Veränderungsprozesse zu reflektieren. Abschließend werden zukünftige Forschungsrichtungen im Rahmen des *OpenEvo Learning Hub* skizziert, einer online Lehr- und Forschungsumgebung, um die in dieser Dissertation vorgeschlagenen Innovationen für den Evolutionsunterricht kooperativ weiterzuentwickeln. Schlussfolgerungen betonen die Notwendigkeit einer stärkeren Zusammenarbeit zwischen WissenschaftlerInnen und Lehrenden, um das Bildungspotenzial der wissenschaftlichen Entwicklungen des 21. Jahrhunderts, inbesondere die zunehmende Interdisziplinarität der Evolutionswissenschaften, voll auszuschöpfen.

(German translation by Susan Hanisch)

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1 Introduction

Advancing evolutionary theory in the 21st century is a robustly interdisciplinary, if not transdisciplinary scientific endeavor. From biology and anthropology, to medicine, psychology, economics, sustainability science, computer science, and many more fields of study, the core concepts of heritable variation and selective retention have been utilized by scientists across academia to understand diversity across natural, social, and artificial worlds. Evolution education, however, remains largely (if not exclusively) a disciplinary endeavor of biology education. This means that educators are left with little guidance on interpreting the broader interdisciplinary applications of modern evolutionary science discourse. In fact, current representations of evolutionary concepts in evolution education may prove challenging for the integration of current interdisciplinary perspectives on evolution. For that reason, there is a need for biology education to take the lead in creating supportive conditions for pedagogical innovations in this space. This thesis engages an educational design research perspective on the systems, practices, and resources that could support or hinder the emergence of teaching evolution as the interdisciplinary science that it is.

In the following sections, I outline the educational design concept and research model that has informed (and co-evolved with) my thesis. I then offer a reflective note on the scale of the goals of this work, and provide a concise outline of the arguments put forth within the chapters constituting this cumulative thesis.

1.1 Educational design concept and research model

At the beginning of my thesis in 2016, my collaborator (Susan Hanisch[1]) and I had developed a syllabus for a teacher education module focused on the behavioral dimensions of sustainable development, from interdisciplinary evolution science perspectives (originally titled *Global Education for Sustainable Development* or *Global ESD*, see www.GlobalESD.org and Eirdosh & Hanisch 2019, the module is now run under the name *Human Behavior & Sustainable Development*). This module was based on our own prior scientific learning and

[1] Susan Hanisch has been my long-term collaborator in this work since prior to the start of my doctoral work, and while all of my individual contributions to this thesis are explicated in detail in *Appendix C*, due to the interdependent nature of our collaboration, I will use "we" and "our" when referring to our shared insights and perspectives within this work, even where I am the sole author in this specific context.

pedagogical intuitions, but we lacked a formal theoretical framework to support our design choices, let alone to drive empirically warranted improvements to the syllabus.

It has only been through an intensive, iterative process of comparing the conceptualizations and aims of our module, with the conceptualizations and aims in the evolution education research and interdisciplinary education research literature, that we have been able to advance the infrastructure for more disciplined design-focused inquiry (see *Chapter 3*) within a coherent paradigm oriented towards teaching evolution as the interdisciplinary science that it is.

It is beyond the scope here to engage a detailed discussion of the broader educational design concept and research model emergent from this thesis, as this is discussed more extensively in our *Teacher's Guide to Evolution, Behavior, and Sustainability Science* (Hanisch & Eirdosh 2020a), as well as on the Global ESD website (e.g. http://research.globalesd.org).

Here I wish only to highlight three guiding principles that have informed my choices in advancing this research program design.

Networked co-design. Improving educational systems is a socially and technically complex process, involving many diverse stakeholders and complex cultural patterns of change and stasis. Educational research, in this context, has broadly been critiqued in terms of how research insights are translated into real-world practice. *Educational design research* (McKenney & Reeves 2018, Mintrop 2020) can be described as one response to these critiques. Within this expansive tradition, concepts such as *Networked Improvement Communities* (NICs, Bryk et al. 2015, LeMahieu et. al 2017), and *Researcher-Practitioner Partnerships* (RPPs, Penuel 2019) have emerged to suggest the need for *networked co-design* of innovations with school stakeholders as a driver of effective implementation, evaluation, and improvement. In this context, a core commitment across this work has been to engage a robust diversity of stakeholders, including scientists, teachers, and students themselves, not simply as participants, but as co-designers of our educational design concept.

Infrastructuring. Supporting educational communities in *networked co-design* is not a simple task, especially in the uncharted landscape of interdisciplinary evolution education. Therefore, a central aim of educational systems improvement in this space must be on creating infrastructure (i.e. *infrastructuring;* Penuel 2019), or creating the tools, resources, processes, institutions, technologies, knowledge, and skills to drive effective implementation, evaluation, and improvement of targeted innovations. In this context, the extensive conceptual clarification, education design concept development, and digital design-based research infrastructure that have emerged from this thesis represent a central commitment towards capacity building through infrastructuring activities.

Long-form research. Finally, infrastructuring for networked co-design is likely to be important for the sustainability of any given educational improvement project (Penuel 2019), critically however, sustaining improvement efforts may have scientific merit beyond the valued improvements themselves.

As co-director of the Max Planck Institute for Evolutionary Anthropology, Richard McElreath (2018), describes:

"Human societies display long-form adaptation. Humans adapt behaviorally, and human behavior requires years to acquire and generations to develop. Long-form behavioral adaptations explain our species' extraordinary diversity and its ecological success. At the same time, the cognitive mechanisms and population dynamics that make longform adaptation possible also make possible evolutionarily novel societies and forms of behavior and technology. Humans have coexisted with these evolutionary novelties for long enough that our genes are adapted to them.

The study of long-form adaptation will benefit from long-form research that is both longitudinal and comparative, allowing it to inform theories of human evolution and the dynamics of human societies. Normal human science lacks the necessary infrastructure."

McElreath is framing this concept of long-form research in the context of the foundational scientific aims of his own field of human behavioral ecology, yet the implications for applied educational design research are at least as significant. Educational design is a model long-form adaptive cultural trait, or at least, that is what societies often seem to (implicitly) hope for. The variability of the *adaptive value* of education, however that may be defined for any given individual or community, is the central outcome that *networked improvement* approaches to *educational design research* seek to address over time. That is, for schooling to be considered *adaptive* for cultural groups (or the planet as a whole), schools definitionally need to consider the nested scales in space and time at which human adaptations are evolving, from within individuals in the immediate moment (*sensu* Wilson & Hayes 2018; Atkins et al 2019), to the evolving institutions that shape and sustain valued innovations across school systems over generations.

Importantly, while the suggestion of using perspectives in cultural evolution science to inform innovations in evolution education is unique (i.e. no substantive precedents for such a view have been found), the implications of such a view are congruent with large swaths of educational design research literature, while also adding uniquely interdisciplinary value to the research landscape. Figure 1 represents our emergent model for educational design research, adapted from the influential McKenney & Reeves (2018), with additional model elements added to clarify our unique research commitments. The cumulative thesis articles are mapped to the approximate area of focus within the model, with the recognition that these are highly interdependent and nonlinear processes.

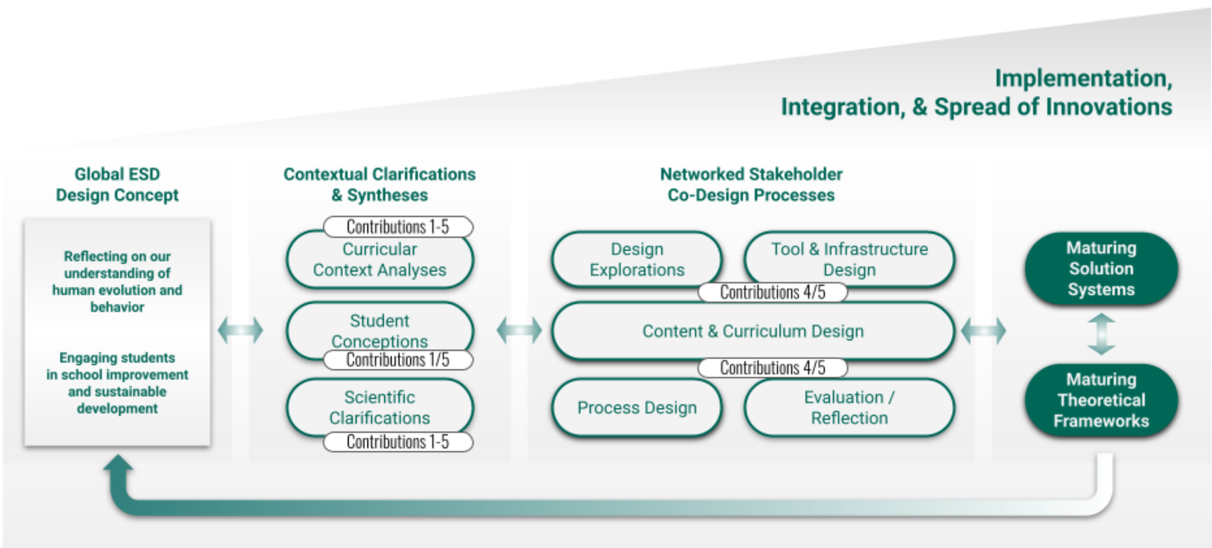

Fig. 1 The Global ESD educational design research model adapted from McKenney & Reeves (2018, fig 3.3). Integrating the Global ESD design concept (Hanisch & Eirdosh 2020a) as a context for contextual clarification, synthesis, and networked stakeholder co-design processes of elements within a maturing solution system and theoretical framework for continued improvement of educational innovations.

Specifically, we have integrated a dual pedagogical focus on *conceptual understanding of human evolution and behavior* (in the tradition of Stern et al 2021), with active *engagement in school improvement and sustainable development* as a high-level unifying thread to organize otherwise diverse work. This process often begins with and/or requires the support of additional contextual and conceptual clarifications. These foundations can then support networked stakeholder co-design processes around specific pedagogical resources. As these resources, tools, lessons, and processes mature, they can be further improved through integration across resources within the ecosystem, and thorough evaluation of efficacy in novel educational contexts.

The articles that have resulted from advancing this process offer an early proof of concept for the potential of this educational design research model for interdisciplinary education innovation grounded in evolutionary and behavioral sciences.

1.2 Notes on the scope of claims and methods within this thesis

Perhaps the most common point of discussion on my thesis throughout this process is the perceived 'ambition' of the aims, with some suggesting that 'teaching evolution as an interdisciplinary science' is perhaps too large a goal, too vast a scope to be productively pursued within the context of a doctoral thesis. For this reason, it is worth some space to clarify and reflect on this scope and how my methods and scientific strategy relate to these ambitions.

In no uncertain terms, a central argument in this thesis is that a prominent mainstream educational conceptualization of evolution, as narrowly defined in *gene-centric* terms (defining the concept of evolution exclusively in terms of changes in allele frequencies), is inadequate for meeting the needs and aims of many students in the 21st century. As described, in Chapter 2.3 (Hanisch & Eirdosh 2020d), we suggest that proponents of this gene-centric view of evolution education are "climbing the wrong mountain" (see Figure 2 below) when it comes to the conceptualizations, aims, and potential of evolution science in the general education context. This claim requires some further critical unpacking to help contextualize the aims and strategic development of this thesis as a whole.

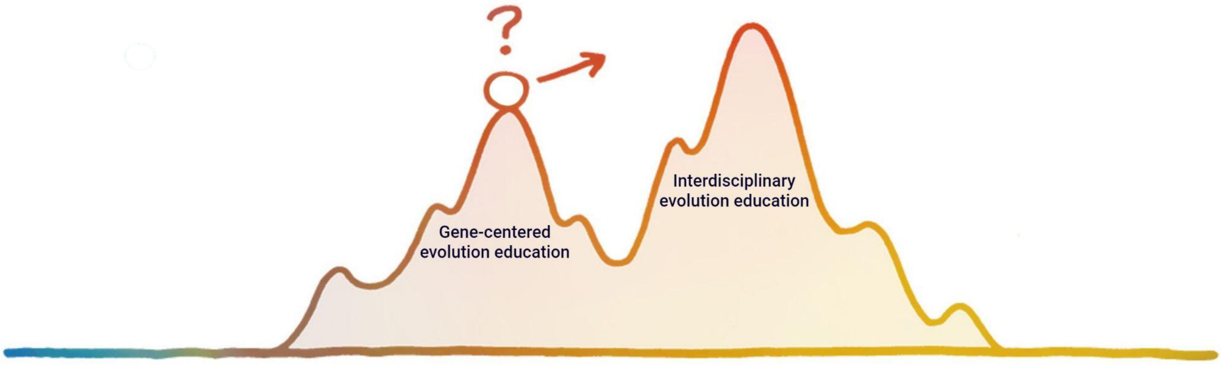

Fig.2 Is evolution education climbing the wrong mountain? (Source: Hanisch & Eirdosh 2020b) The metaphor of a fitness landscape (commonly used in evolutionary biology and equally useful in cultural evolution science) to illustrate how progress in evolution education research might be inherently constrained to a lower-level potential that is defined by gene-focused conceptualizations of evolution, compared to the higher-level global potential that might present itself by embracing a more generalized, interdisciplinary conceptualization of evolution. Here, fitness peaks may correspond to varying degrees of cultural acceptance or depth of transferable conceptual understanding of core evolutionary theory. Figure adapted with permission from Jurgen Appelo: https://www.flickr.com/photos/jurgenappelo/with/5201851938/

In the past ~year since this claim was published in *Evolution Education and Outreach*, we have gotten a *diversity* of positive and critical feedback from our colleagues in evolution education research and the evolution sciences on this metaphor of “climbing the wrong mountain”. This diversity of responses itself offers an important window into the context in which this thesis was developed. We have been told by some that it is a timely and much-needed clarification of the conceptual landscape. Others have suggested that our interdisciplinary approach is fine “for advanced students”, but suggest that students must *first* climb the mountain of gene-centric evolution understanding. By still others (including some reviewers), we have been told it may be a “straw-person argument”, that we are “battling against windmills”, that our characterization of a gene-centric view of evolution is simply “not what biologists actually believe”. In stark contrast to this, others (with equal credentials) have suggested that our characterization of gene-centric evolution education *is* accurate, but simply put, gene-centrism *truly is* the (only) proper mountain for evolution educators to climb. At the most extreme, one well-intentioned evolution education advocate has attempted to construe our critique of gene-centrism as akin to creationism. This short portrayal of the diversity of reactions we have encountered highlights that the world of evolution science and education is indeed conceptually diverse, perhaps more so than many in our field realize. That is a point I wish to emphasize here as a key context for understanding the metaphor of “climbing the wrong mountain” and our related critique of gene-centrism in the education context.

The aim of the *wrong mountain* metaphor is not to suggest that *all* or even *most* evolution educators and evolution education researchers are deeply committed “gene-centrists”. Our experience over the last decade of engagement in these discussions makes it clear that is not the case (though the actual diversity of beliefs among evolution education experts is a subject in need of more formal study). Rather, our aim in invoking this metaphor is to allow all of us within the evolution education community to take a step back and look more reflectively at the full conceptual landscape of evolutionary conceptualizations of the world around us, and ask the big questions about the pedagogical and scientific value of how we are helping younger generations understand the emergence and persistence of diversity in populations of diverse agents.

As we have discussed extensively across the range of scientific outputs found in *Appendix B*, the actual conceptual diversity of our field is significant and not always explicitly reflected upon. This is true even within popular conceptual frameworks being used within research contexts (see especially the discussion on UC Berkeley’s Understanding Evolution K-16 Conceptual Framework within the pre-print, Hanisch & Eirdosh 2020c). Hence, it is important to reflect that when we have described evolution education as, broadly, “climbing the wrong mountain”, the suggestion is not that the majority of our field stands perched at the peak of optimal teaching for an exclusively gene-centric model of evolution and we all need to move towards the peak of interdisciplinary approaches. Rather, we would suggest that the overwhelming majority of our field reside somewhere within the valley between a truly gene-centered and a more interdisciplinary, trait-centered model of evolution education. That is, the overwhelming majority of colleagues that we interact with occupy a diverse middle ground space of positions, sometimes with only limited metacognitive awareness of their own stance within the broader scientific landscape. Some may lean more towards or be more comfortable engaging with gene-centric perspectives while variously tolerating or even espousing interest in more interdisciplinary conceptualizations. Others may be more strongly interested in the interdisciplinary dimension, but lack the support to climb very high on the emergent landscape, and so they remain unable to venture too far from the constraints of this less than clear conceptual middle ground. To be clear, we do routinely encounter what might be called ‘strong gene-centrists’, individuals who are certain that the only properly scientific conception of evolution must be constrained to a change in allele frequencies, both inside and outside of biology education (many a humanities scholar / educator as well will argue for evolutionary thinking to remain constrained to "biology"). Suffice it to say that my experience in the field has suggested there is a powerful middle-ground contingent interested in the conceptual clarification of more pluralistic perspectives.

Against this context, an admittedly ambitious higher-level goal of this thesis is to explicitly support a more *intentional process of cultural evolution* (*sensu* Wilson & Hayes 2018; Atkins et al. 2019) within the evolution education research community, and broader global interdisciplinary education innovation communities. While it is beyond the scope of this thesis to scientifically measure or model this cultural evolution (see *Chapter 3*), what has been accomplished is the development of *conceptual clarifications* and *infrastructure* for education design research aimed at empowering global innovators and researchers to collectively drive our own pedagogical evolution into the future. That is, the tools and frameworks produced in the course of this work now allow new interdisciplinary *variants* in lesson or curriculum design to *emerge* and be *transmitted*, *adapted*, and *selectively retained* within local classroom contexts around the world. That is, this thesis has taken some needed first steps in supporting a more intentional cultural evolution of teaching and learning about human evolution, behavior, cognition, and culture.

1.3 Overview of the cumulative thesis

This thesis begins with the everyday understanding of students and teachers regarding the evolved capacities for humans to cooperate, and concludes with tools and research infrastructure to help students and teachers evolve a direction in evolution education. In between, an interdisciplinary synthesis and theoretical framework are developed that suggests a need for new conversations about the scope and purpose of evolution education in the general education curriculum.

First, we might ask: *why should it matter if we teach evolution as an interdisciplinary science?* In Chapter 2.1 (Hanisch & Eirdosh 2021a), we offer a small classroom-based study on student and teacher conceptions of cooperation and sustainable resource use dynamics across chimpanzees and 6-year-old humans. We find that German students, and perhaps even more so, German pre-service biology teachers, tend to view chimpanzees, and not humans as the more 'cooperative species', a view in stark opposition to insights from evolutionary anthropology. The reasons for these apparently common beliefs are complex, and, perhaps more daunting, the educational remedies for supporting a more scientifically adequate view are less than clear. Thus, in Chapter 2.2 (Eirdosh & Hanisch 2020) we ask the question: *can the science of Prosocial be a part of evolution education?* By exploring an emerging scientific community that is grounded in an interdisciplinary evolutionary model of human cooperation, *Prosocial*, we suggest that current conceptualizations dominant in evolution education and evolution education research may be less than adequate to engage with modern interdisciplinary conceptualizations of evolutionary processes beyond genetic change alone. This contribution also further contextualizes the community-based research model documented in Chapter 2.5 (Eirdosh & Hanisch 2021, discussed below)

Having outlined some core challenges and conceptual issues, Chapter 2.3 (Hanisch & Eirdosh 2020d) structures a roadmap for understanding the educational potential of teaching evolution as an interdisciplinary science. After an extensive discussion of the core challenges facing evolution educators and education researchers, this work suggests that, to the degree that the evolution education community adopts a strongly *gene-centric* conceptualization of evolutionary change (defining evolution *solely* in terms of change in allele frequencies), this is the degree to which the community can be described as 'climbing the wrong mountain', and that instead, the field should focus on a more transferable conceptual clarification of evolution as a change in trait frequency within complex adaptive systems (fig. 1). That is, we should be focusing on teaching conceptualizations of evolutionary change congruent with modern interdisciplinary evolution science perspectives. This work represents the theoretical foundation for this thesis.

To ground these higher-level theoretical arguments in classroom practice, I then offer two classroom-based case studies. The first, Chapter 2.4 (Hanisch & Eirdosh 2020c), describes a novel teaching tool for human evolution educators, that of *causal mapping*. The idea of box and arrow causal maps, in general, is pervasive in education. What we have added is a conceptual framework for helping students integrate evolutionary and developmental processes across the full diversity of *causal domains* (e.g. genes, bodies, brains, behavior, abiotic and social environments, etc.). This teaching tool demonstrates the viability of engaging secondary school students and teachers in interdisciplinary conceptualizations of evolutionary theory, while also providing a structure to navigate classic evolution understanding challenges such as those related to the nature of teleological reasoning, goal-directed behaviors, as well as population and selectionist thinking, in evolutionary explanations.

The final publication within this cumulative thesis, Chapter 2.5 (Eirdosh & Hanisch 2021), offers a case study from exploratory work within our *Community Science Lab* in the Department of Comparative Cultural Psychology at the Max Planck Institute for Evolutionary Anthropology. Developed during the first Covid-19 lockdowns during the spring of 2020, the *Evolving Schools* project was launched to simultaneously elevate student voice in school improvement aims, while also driving reflection on scientific perspectives on the evolution of teaching and learning. Exploratory findings from this case study suggest the suitability of *teaching and learning* as a conceptual focus within evolution education. Evolutionary anthropologists recognize the likely significant role of teaching and learning across hominin evolutionary history (see Sterelny 2012). In this context, the concepts of *teaching and learning* represent traits of interest for understanding gene-culture co-evolution, traits that are definitionally close to the everyday lives of students. Our case study suggests that secondary school students may hold a number of adequate evolutionary concepts in this domain without instruction, and may also benefit from more explicit and critical reflection on how they utilize evolutionary concepts in explaining the efficacy of schools and the nature of school improvement.

I frame conclusions and future directions in this work through our emergent project, OpenEvo, for supporting the evolution of an open, networked, and interdisciplinary evolution education research community. This project represents the final practical outcome of the knowledge synthesis represented by this thesis, and in this way offers a *proof of concept* for the impact of this analysis as a whole on the development of needed structures for supporting evolution education research in the 21st century.

2 Cumulative articles

This chapter contains the five published articles constituting this cumulative thesis.

2.1 Contribution 1

Are humans a cooperative species?

Challenges & Opportunities for Teaching the Evolution of Human Prosociality

Hanisch, S., & Eirdosh, D. (2021). Are Humans a Cooperative Species? Challenges & Opportunities for Teaching the Evolution of Human Prosociality. The American Biology Teacher, 83(6), 356-361.
http://dx.doi.org/10.1525/abt.2021.83.6.356

FORMULAR 1

Manuskript Nr. 1

Titel des Manuskriptes: Are Humans a Cooperative Species? Challenges & Opportunities for Teaching the Evolution of Human Prosociality

Autoren: Susan Hanisch and Dustin Eirdosh

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Status: Published

Anteile (in %) der Autoren / der Autorinnen an der Publikation (anzugeben ab 20%)

Autor/-in	Konzeptionell	Datenanalyse	Experimentell	Verfassen des Manuskriptes	Bereitstellung von Material
Hanisch	20%	50%	0%	80%	0%
Eirdosh	80%	50%	100%	20%	100%

FEATURE ARTICLE

Are Humans a Cooperative Species? Challenges & Opportunities for Teaching the Evolution of Human Prosociality

SUSAN HANISCH, DUSTIN EIRDOSH

Abstract

Evolutionary anthropologists commonly describe humans as a highly cooperative species, based on our evolved socio-cognitive capacities. However, students and the general public may not necessarily share this view about our species. At the same time, fostering our ability to cooperate is considered a key foundation for achieving sustainable development, and students' understanding of the conditions that enable or hinder cooperation is therefore an important learning goal in sustainability education. In this article, we describe a small classroom activity that explored students' and preservice biology teachers' preconceptions about the human capacity to cooperate around shared resources in comparison to the capacity of our closest relative, the chimpanzee. Results indicate that students and teachers had limited knowledge about the evolved human capacity for cooperation around shared resources in small groups, most often viewing chimpanzees as more capable of cooperation and sustainable resource use. Based on the results of this classroom intervention, we highlight important learning opportunities for educators in biology on teaching human evolution and human behavior, particularly as related to current challenges of sustainable development.

Key Words: *behavior; comparative research; cooperation; human evolution.*

○ Introduction

Evolutionary anthropologists commonly describe humans as a highly cooperative species – whether it is in contributing to the group, sharing resources and information, or helping others, humans across cultures seem to care about the well-being of others, about fairness of outcomes, and are willing to enforce norms of cooperation even with a cost to themselves (Henrich et al., 2006; Bowles & Gintis, 2011). There is also wide agreement in the evolutionary and developmental human sciences that our species-typical capacity to cooperate in groups around shared goals and resources runs deep within our hominid evolutionary history (Tomasello, 2009), and that such social tendencies develop early in life (Warneken & Tomasello, 2009).

Importantly for current societal issues, cooperation is also considered a major prerequisite for achieving ecological, social, and economic sustainable development, while our ability to cooperate can be hindered by certain proximate conditions (e.g., Messner et al., 2013; Wilson et al., 2013). Thus, understanding the behaviors and conditions that allow humans to cooperate around the sustainable management of shared resources and other shared goals can be considered a foundation in education for sustainable development, such as for developing cooperation competencies in students (UNESCO, 2017).

However, currently not much is known about whether students, teachers, and everyday citizens have an adequate conceptual understanding of the cooperative abilities in our species and their proximate and ultimate causes. For example, da Silva Porto et al. (2015) investigated Brazilian undergraduate students' conceptions about the causes of human social behavior on a nature-nurture spectrum (i.e., from more evolutionary and genetic causes to more experience-based and cultural causes). The majority of students considered human social behaviors to be mostly influenced by nurture and less by nature. The authors suggest that this may be due to the absence of human behavior as a theme in the biology curriculum of Brazilian high schools. Similarly, in the United States, the theme of human behavior is explicitly excluded from the *Next Generation Science Standards* (NGSS; National Research Council, 2012; NGSS Lead States, 2013), while the evolutionary and biological causes of human behavior are explicitly excluded from the core of U.S. social studies standards (National Council for the Social Studies, 2013).

> *"Students were less likely to explain human social behavior with reference to evolutionary causes and more likely with reference to developmental and cultural causes."*

In the German context, human behavior is a theme in high school biology curricula, but it is unclear to what degree evolutionary causes of human *social* behavior are explored

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in classrooms, particularly in comparison to the behavior of other species and in terms of implications for sustainable development.

Here, we present results of a classroom intervention that shed further light on German secondary students' and preservice biology teachers' beliefs and causal explanations about the nature of cooperative behavior in humans compared to a nonhuman primate. Based on these results, we highlight important learning opportunities for educators in biology on the themes of human evolution, human behavior, and sustainability.

○ Methods

In order to elicit students' conceptions regarding the nature and causality of human cooperative behavior, a series of studies (Koomen & Herrmann, 2018a, b) was chosen as a focal topic for a brief written assignment in classrooms. The studies investigated and compared behaviors of (1) pairs of six-year-old children and (2) pairs of semi-wild adult chimpanzees when faced with a common-pool-resource problem (Figure 1). The experimental setup was designed to represent conditions of common-pool-resource dilemmas, including a limited renewable resource and shared access to the resource. Such dilemmas – between individual short-term interest to maximize resource use and collective long-term interest to sustain the shared resource – have been referred to as the "tragedy of the commons" since the publication of Garrett Hardin's famous article of that name (Hardin, 1968). Such dilemmas are at the heart of many societal sustainability problems and are studied in ecology and evolutionary biology to understand cooperation dynamics across species (e.g., Rankin et al., 2007; Poteete et al., 2010). In these studies, chimpanzee dyads tended to be less successful in using the resource for as long as possible; tended to share resources less equally, due to dominance-submission behaviors; and tended to perform worse with each trial, in comparison to children.

Besides the relevance to sustainability issues, the study series was chosen because a scientifically adequate prediction and interpretation of results rests upon both ultimate and proximate explanations of cooperative behavior of the two species.

Participant written assignments were conducted in classroom settings with a total of 180 students, spanning high school classes (grades 6–10) across four German schools as well as preservice biology teachers at the University of Leipzig. Classroom interventions were implemented by the authors and by two preservice biology teachers whose results we include here (Herr, 2018; Regner, 2018).

The experiment series was explained to participant groups with the help of a short presentation (5–10 minutes), emphasizing important conditions of the experiments and the common-pool-resource device, and the questions the researchers were interested in. The participants were then given the opportunity to ask a few questions they might have (e.g., regarding other conditions of the experiment they would like clarification on). Common questions concerned the age of the chimpanzees (including relative maturity compared with children), whether children or chimpanzee pairs knew each other before the experiment, or whether children of the same or different sexes were paired together.

Then the assignment sheet was handed out and participants were given 5–10 minutes to answer the following questions:

- Which of the two species do you think was more successful in using the resource sustainably? (Children / Chimpanzees)
- Why do you think this species was more successful?
- Why do you think the other species was less successful?

Participants were given an opportunity for discussion with their neighbors, since the activity was not meant as an assessment tool but as an interesting conversation starter for the theme of human evolution. Consequently, students' answers do not necessarily represent individual conceptions, but may nonetheless reflect a general pattern of variation within and across participant groups. After assignment sheets were collected, answers were discussed in the group and the actual results of the experiment were presented to the group.

Collected assignment sheets were transcribed and analyzed by the two authors using a theory-based thematic analysis followed by an inductive-deductive coding process (Table 1). Explanations included various causal factors ranging from evolutionary to developmental and proximate causes, thus covering important classes of causes explored in behavioral biology (Mayr, 1961; Tinbergen, 1963). Explanations also often included some essentialist statements about the nature of the two species.

Since there were qualitative differences in the kinds of explanations given for the two species, partly different categories were

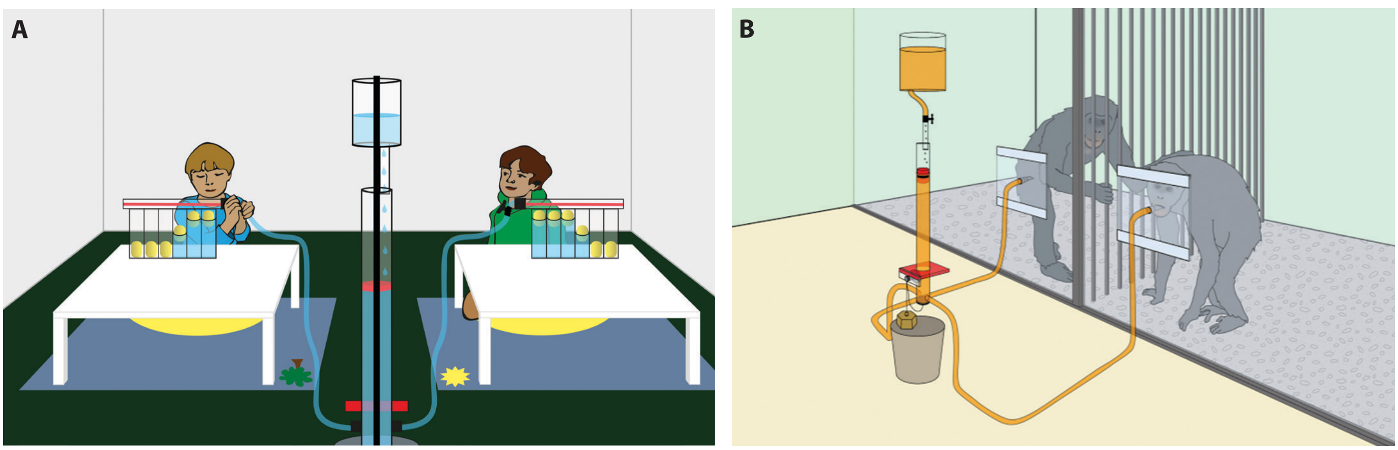

Figure 1. Experimental setup of the experiments with (**A**) children and (**B**) chimpanzees.

Image sources: (A) MPI-EVA Media inspired by Koomen & Herrmann (2018a); (B) Koomen & Herrmann (2018b).

Table 1. Types of causes by causal class that were used to analyze answers in an inductive-deductive approach, with example participant quotes for each code.

Category	Example Quotes
Explanations for why chimpanzees will be more successful	
Cooperative or sustainable by nature	"By nature, chimpanzees are not 'selfish,' meaning they can easily divide scarce resources. They also learned this in the wild (or inherited from their ancestors)."
Intelligence/understanding	"I think the chimpanzees will understand the bigger picture better."
Knowing the partner	"Chimpanzees will be more successful because they come from the same group."
Other (e.g., hierarchy, maturity, experience)	"The chimps are grown-ups." "They live in a hierarchy so the higher-ranking will control it."
Explanations for why children will be more successful	
By cooperative nature	"Cooperation is already more pronounced in *Homo sapiens*."
By understanding	"They can understand the new situation faster."
By education, culture, experience	"They have learned the principle of sharing at home."
By ability to communicate	"Because they can communicate."
Other (e.g., more self-regulation, shyness)	"They can regulate themselves better than the chimps." "They will be shy."

formed for each species. For the chimpanzees, many explanations described essential qualities or mentioned evolutionary causes or survival needs in nature. It was often not clear whether participants referred to the experience or characteristics of the specific individuals participating in the experiments or of the species in general (e.g., "They have to share in nature"). Therefore, we placed any such general and ambiguous explanations into an overall "cooperative by nature" category. Other explanations clustered around the notion that chimpanzees will understand the problem better or the fact that they already know each other.

In regard to human children, explanations referenced some essential qualities of humans and/or children, developmental factors such as age, education, and experience, their ability to understand, and their ability to communicate. For each species, a category of "other explanations" included a range of factors, such as the maturity of chimpanzees, the role of hierarchy, shyness of the children, or factors of the proximate situation of the experiment.

Table 2. Quantitative results of participant predictions about the outcomes of the experiments by participant group.

Participant Group	*n*	Species Predicted to Be More Successful in the Cooperation Task	
		Children (%)	Chimpanzees (%)
Grade 6[a]	17	35	65
Grade 10[b]	103	23	77
Preservice biology teachers	60	20	80
Total (average %)	**180**	**(23)**	**(77)**

[a] Data from Regner (2018).
[b] Includes (*n* = 76) data points from Herr (2018).

○ Results

The majority of participants predicted that chimpanzees would be more successful at cooperating in this experiment (Table 2). Among the explanations for why chimpanzees would be more successful (Table 3), the most dominant conception was a notion that chimpanzees would be more cooperative or sustainable, due to their evolved instinct, need to survive, or need to live and share food in groups and/or to their experience with limited resources in nature. A relatively large number of students explained that chimpanzees would understand the situation better. A range of responses also demonstrated anthropomorphic reasoning, ascribing human-like traits to the chimpanzees, which evolutionary anthropologists would generally agree are more pronounced in humans (and already present in six-year-olds) than in chimpanzees – such as self-regulation, a sense of community, and the ability to negotiate for equal outcomes, to think about the future, to coordinate actions. A few participants accurately predicted that the success of chimp dyads would be due to dominance strategies and unequal resource distribution.

Table 3. Distribution of types of qualitative answers among participants who rated chimpanzees as more successful, with a total of 124 explanations. Note that percentages per participant group do not add up to 100% because several types of answers were sometimes given per participant.

	Types of Explanations for Why Chimpanzees Would Be More Successful: *n* (%)			
	Nature	Understanding	Knowing the Partner	Other
Grade 6[a]	4 (40)	4 (40)	0	2 (20)
Grade 10[b]	58 (78)	18 (23)	12 (16)	13 (18)
Preservice biology teachers	32 (80)	4 (10)	0	6 (15)
Total (average %)	94 (76)	26 (21)	12 (10)	21 (17)

[a] Data from Regner (2018).
[b] Includes (n = 76) data points from Herr (2018).

Table 4. Distribution of types of qualitative answers among participants who rated children as more successful, with a total of 40 explanations. Note that percentages per participant group do not add up to 100% because several types of answers were sometimes given per participant.

	Types of Explanations for Why Children Would Be More Successful: *n* (%)				
Participant Group	Nature	Understanding, "Smartness"	Education, Experience	Ability to Communicate	Other
Grade 6[a]	0	4 (67)	2 (33)	0	0
Grade 10[b]	0	15 (65)	5 (22)	6 (26)	3 (13)
Preservice biology teachers	2 (18)	3 (27)	1 (9)	6 (55)	3 (27)
Total (average %)	2 (5)	22 (55)	8 (20)	12 (30)	6 (15)

[a] Data from Regner (2018).
[b] Includes (n = 76) data points from Herr (2018).

Among participants who predicted that children would be the better cooperators in this task, explanations tended toward causes consisting of rational understanding, learning and cultural experience, and ability to communicate (Table 4). We found *two* explanations among preservice biology teachers mentioning a pronounced cooperation in the *Homo* line; thus, these were the only two conceptions from the participant pool that can be considered most in line with scientific conceptions.

There were some stark differences in the distribution of explanations across the age groups, which may have been influenced by the kinds of conditions of the experiment that were illuminated by student questions in each group (such as whether partners knew each other).

Further information about qualitative results and example student quotes can be found in the Supplemental Material with the online version of this article.

○ Discussion

Two results of our classroom intervention are noteworthy: quantitatively, the majority of students considered chimpanzees to be more cooperative than six-year-old children, and qualitatively, there was a difference in the kinds of explanations that were offered for the behaviors of the two species. Results of our investigation comport with results obtained by da Silva Porto et al. (2015), namely that students were less likely to explain human social behavior with reference to evolutionary causes and more likely with reference to developmental and cultural causes.

Future studies may want to investigate the prevalence of different participant conceptions in a more controlled fashion, since our study did not aim to do this and was designed as a classroom activity that encouraged discussion among participants. It would also be interesting to investigate the predictions and explanations about this experiment of students and teachers in the United States and other cultures.

Why Are the Explanations of Chimpanzee & Human Behavior Qualitatively Different?

Research on how people tend to explain human behavior shows that people do not seem to invoke evolutionary or broader historical causes when explaining human behavior. For example, in their framework of the factors that people refer to when explaining human behavior, Böhm and Pfister (2015) consider that *dispositions* "are assumed to mark the end of a causal search, to be particularly satisfactory explanations, and to serve as ultimate explanations that do not raise any further questions."

Of course, in biology, dispositions are hardly considered "ultimate explanations" that end a causal search; if anything, they can mark the *beginning* of a causal search into the deeper evolutionary histories and functions of the behavioral dispositions of living things. When predicting or explaining the differences or similarities between human and animal behavior, such deeper evolutionary causes are required. However, it appears that students (and teachers) need support to reason adequately about evolutionary causes of animal social behavior, and particularly to also include *evolutionary* factors in the explanation of *human* social behavior.

Why Do Students & Teachers Tend to Think That Chimpanzees Are More Cooperative?

One class of factors that might help answer this question is what we have come to call "invisible cooperation" – even though cooperation pervades our everyday lives, it may be taken for granted to such a degree that people do not regard these human characteristics as something that requires an (evolutionary) explanation or as something that distinguishes us from other primates. Furthermore, everyday feats of human cooperation are not what we commonly observe in the media and daily news, which rather emphasize conflict and violence in our societies. Additionally, our current challenges of sustainable development may lead to a cultural conception that the causes of such issues lie in our human nature – after all, we do not commonly hear about chimpanzees polluting their environments or overusing their resources. In fact, however, chimpanzees *have* been observed to overhunt a monkey species to near extinction (Lwanga et al., 2011), and chimpanzees have been observed to show rates of violence and aggression two to three orders of magnitude higher than in human hunter-gatherer groups (Wrangham et al., 2006). Further, economic models of humans may have pervaded cultural conceptions of humans as selfish, profit-maximizing creatures (*Homo economicus*), contributing to the invisibility of everyday human cooperation.

Education may be another plausible cause of these observed patterns. For example, a content analysis of 23 German high school biology textbooks (S. Hanisch & D. Eirdosh, in review) indicates that the role of cooperation in the evolution of our species may be little emphasized, compared to other factors such as large brains and individual intelligence. Furthermore, in sections on behavioral ecology and cooperation, we find that humans are hardly ever mentioned as an example of a cooperative species. Comparative behavioral experiments are also rarely featured as methods used by scientists to explore the origins of human behavior.

Similarly, as we highlighted in the introductory section, in the NGSS, human behavioral sciences are explicitly excluded and are considered to be covered more by the social studies disciplines. At the same time, the themes of relationships in ecosystems and animal group behavior in the NGSS may not be transferred to the understanding of human behavior, while the theme of evolution does not reference the role of cooperation and interdependence (NGSS Lead States, 2013). Conversely, the social studies disciplines may not treat human behavior from a biological perspective, especially in comparison to other species and in regard to exploring the evolutionary causes of human behavior. We argue that this ambiguity regarding where human social behavior is situated (or not situated) in the curriculum may create a kind of conceptual blind spot in students and (biology) teachers when it comes to understanding and explaining human social behavior.

Our conceptions about human nature have a strong influence on our attitudes and behaviors toward ourselves and other humans in social life. For example, a view that humans are predominantly selfish has been shown to lead to less cooperative behavior (Frank et al., 1993). Thus, our finding that a majority of high school students and teachers seem to have a quite negative conception about human nature could be considered a rather alarming phenomenon. Overall, a cultural narrative of humans as selfish or greedy may have influenced participants' intuitive notions about what it means to be human, based on the aspects of human nature that are emphasized in the media, in economics, in biology and other disciplines, and in narratives about the causes of our current sustainability challenges.

Learning Opportunities for Evolution & Sustainability Education

Our findings demonstrate that students need support to construct a scientifically adequate understanding of human social behaviors and their evolutionary, cultural, and developmental origins. Here, we offer suggestions for U.S. biology teachers regarding how they might provide students this support, particularly within the topics and core ideas of the NGSS.

(1) Disciplinary Core Idea LS2.D: Social Interactions and Group Behavior (NGSS Lead States, 2013) provides students an opportunity to compare human and other animal social behaviors, their functions and evolutionary origins, toward a critical understanding of the claims that humans are a highly cooperative species and that cooperative social behavior pervades our lives. The classroom intervention presented here, and similar cross-species cooperation experiments, can offer productive teaching tools around this set of core ideas.

(2) Link the topics of natural selection and evolution with the core idea of Social Interactions and Group Behavior in order to provide students with the opportunity to explore the conditions that favor the natural selection of group behavior. In a unit on human evolution, emphasize the role of cooperation and prosociality in the evolution of our species' behavior and cognition (e.g., cooperative hunting, cooperative foraging, resource sharing, moral cognition, teaching and social learning; e.g., Burkart et al., 2009; Hayes & Sanford, 2014).

(3) Link the themes of cooperation and group behavior to the NGSS theme of Human Sustainability and to themes in social studies. The social dilemma of the "tragedy of the commons," inherent in the experimental design of this lesson, is a central model that highlights the challenges of cooperation toward sustainable development. From natural resource use and climate change to cooperative learning and peer groups at school, cooperation dilemmas pervade the many challenges that students will experience within their lifetimes. The lesson presented here can serve as an introductory activity for students to explore this challenge and the conditions and behaviors required to overcome it (Wilson et al., 2013; Atkins et al., 2019).

To support educators in these directions, we have begun to advance a range of open-education resources that integrate the themes of human evolution, behavior, and sustainability (http://teaching-materials.globalesd.org).

○ Conclusions

Our results suggest that insights into the nature of human social behavior and its evolution that have been gained in recent decades have not been sufficiently translated into educational practice and/or cultural knowledge, at least among the German populations of students and biology teachers investigated in this study. This gap in understanding could have deleterious effects on how students perceive and act in social situations throughout their lives, and on how effectively they may act toward collaboratively solving sustainability problems on local to global scales.

Overall, the behavioral sciences offer a wide range of cross-species, developmental, and cross-cultural experiments and observations that can serve as engaging content that allows students to construct more accurate and helpful narratives about the capacity and conditions for humans to cooperate around sustainable resource use and many other shared goals. We invite readers to implement the lesson presented in this article in their classrooms toward these ends.

○ Supplemental Material

The following resources are available with the online version of this article:

- "Chimpanzees or Children – Who Is Better at Sharing Resources?" Information and materials.
- "Are Humans a Cooperative Species? Challenges and Opportunities for Teaching the Evolution of Human Prosociality." Twenty-two data tables from our study.

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2.2 Contribution 2

Can the science of Prosocial be a part of evolution education?

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FORMULAR 1

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Eirdosh	80%	N/A	N/A	80%	N/A
Hanisch	20%	N/A	N/A	20%	N/A

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Evolution: Education and Outreach

BOOK REVIEW

Open Access

Can the science of Prosocial be a part of evolution education?

Dustin Eirdosh* and Susan Hanisch

Abstract

We provide a brief overview of *Prosocial: Using Evolutionary Science to Build Productive, Equitable, and Collaborative Groups* by Paul Atkins, David Sloan Wilson, and Steven Hayes. The book offers a range of promising content for evolution education, and yet also highlights core conceptual challenges in modern evolution science discourse that educators and researchers aiming to improve evolution education may find beneficial to strategically engage with as a scientific community. We discuss these challenges and opportunities with a view towards implications for evolution education research and practice.

Keywords: Human evolution, Cultural evolution, Multilevel selection theory, Tragedy of the commons, Cooperation

Introduction

Evolutionary anthropologists often describe humans as an ultra-social primate, a highly cooperative species with elaborated capacities to work together at scales of social organization beyond our direct genetic relatives. Despite this scientific perspective, we face the practical reality that many of the modern world's greatest challenges, from climate change to sustaining global democracies, are the result of a failure to cooperate across multiple levels of societal organization. The book *Prosocial: Using Evolutionary Science to Build Productive, Equitable, and Collaborative Groups* by Atkins et al. (2019) offers a unique mix of evolutionary theory combined with practical tools for strengthening cooperation in groups, offering a perspective that may have relevance to the teaching of evolution in general education. This review provides a brief overview of the content of this recent work, and frames some considerations of the challenges and opportunities it presents to the evolution education community.

A note on terminology used in this review: the term "prosocial" refers to a highly general concept in the evolution and human behavioral sciences. In this review the capitalized term *Prosocial* refers to the conceptual framework and applied research processes outlined the the book of the same name. This is to say, *Prosocial* is more than a book, it is also an applied research program and research community that builds on foundational perspectives from evolutionary theory. The *Prosocial* book is merely the latest form of communication to emerge from these efforts, and for these reasons we will use the term *Prosocial* somewhat interchangeably to refer to both the content of the book and conceptual framework it seeks to communicate.

The *Prosocial* book is divided into two parts. Part one offers a conceptual clarification of how evolutionary theory relates to the everyday cooperation dynamics that modern humans live within. Part two then provides more detailed insights into a set of practical tools and principles for the analysis and influence of cooperation within modern human groups. The aim of this review, more than providing a short summary of the content, is to reflect on the potential relevance of the conceptualization of evolution science for evolution education. Thus, the following content summaries are intended only to contextualize the broader review.

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Part 1: Concepts and principles

The first part of the book provides a very readable overview of the historical and conceptual issues that underpin the Prosocial methods. As will be discussed further in the concluding section of this review, the theoretical basis of Prosocial offers some unique challenges and opportunities for the evolution education community. The summary here will provide a roadmap to the relevant issues discussed further below in the section on relevance to evolution education.

Multilevel and multidimensional evolution

The authors have adopted and articulated a very specific conception of evolution that may require some translation and reflection for many in the field of evolution education. Drawing on diverse yet interrelated fields of evolutionary anthropology, organizational psychology, and contextual behavioral sciences, *Prosocial* integrates current theoretical developments in both biological evolution and cultural evolution. This is framed as a multilevel and multidimensional approach to evolutionary analysis (Atkins et al. 2019, p. 10).

By multilevel, the authors mean that evolutionary processes occur at multiple scales of biological and sociocultural organization, from the genome to multi-group populations. This perspective suggests that evolutionary analyses must therefore include tools for identifying and weighing which levels are most relevant within a particular context. This perspective is mostly derived from David Sloan Wilson's work advancing Multilevel Selection Theory as a particular accounting scheme for previous conceptions of group selection, kin selection, and related approaches that aim, among others, to explain the existence of altruistic or prosocial behaviors in the biological world (Atkins et al. 2019, p. 12). Evolution educators familiar with the group selection controversy may find this book lacking an extensively detailed discussion of the conceptual issues underlying such on-going discourse. However, the authors do include an accurate if concise narrative of the history of such thinking from Darwin through today's formalized models, and use research examples to accessibly illustrate this otherwise complex theoretical construct of key importance to evolutionary theory.

Where multilevel evolution expands our conception of selection, the authors argue that a multidimensional perspective can expand our notions of inheritance. Often in evolution education we make a sharp dichotomy between gene and environment, with heritable genetic information being selected by environmental conditions. This is not inaccurate, but only incomplete (Atkins et al. 2019, p. 16). Building on work from evolutionary biologists within the broader discourse on the Extended Evolutionary Synthesis (c.f. Jabłonka and Lamb 2006; Uller and Laland 2019), the authors argue that well-rounded evolutionary analyses should account for the interactions among multiple streams of inheritance; genetic and epigenetic, as well as individual and cultural learning. The authors take aim at more traditional gene-centric models of evolutionary change in which evolutionary change is reduced to change in gene frequency, rather than trait frequency. This is a potentially contentious stance for the evolution education community which we take up in the concluding section of this review.

Homo economicus and the tragedy of the commons

Shifting from foundational biological sciences into more interdisciplinary thinking about socio-economic organization of human societies, the authors bring in several core concepts that are equally contentious in mainstream social science discourse and yet are likely to be of central importance for teachers and students wishing to develop a coherent conception of how our understanding of the human condition relates to how we shape our societies and cultures.

In chapter two, the story of Elinor Ostrom, the first woman to win the Nobel Prize in economics, is presented with the broader history of the *Tragedy of the Commons* and economic models of human behavior. Through cross-cultural studies and a multiple methods approach (see Poteete et al. 2010), Ostrom and colleagues demonstrated that humans do have the capacity for sustainable, democratic governance of shared natural resources (i.e. common-pool resources), but only under certain conditions. Ostrom's model revealed eight *Core Design Principles* (see Fig. 1) for which groups that are successful in managing shared resources tend to have developed effective mechanisms for their implementation.

The authors reflect on Ostrom's work in comparison with the out of date economic model of human behavior often called *Homo economicus,* describing the *rational economic man*, as if he were a species in his own right (Atkins et al. 2019, p. 26). Homo economicus is self-interested and calculates his behavior around this self-interest, whereas *Homo sapiens*, it is pointed out, acts much more like the actors within the common-pool resource contexts that Ostrom studied. The implications of these two models of human behavior is significant in current human science discourse, and may be equally significant for the aims and concepts framed under evolution education.

Evolution and behavioral sciences

This part of the book concludes with a deeper dive into core concepts linking evolution and behavioral sciences. For educators or academics who may think of

Fig. 1 Core Design Principles for the Cooperation of Groups (adapted from Atkins et al. 2019)

"behaviorism" as an outdated science focused on coercive manipulation of rats in cages, the section offers a novel and more nuanced view into current thinking in the behavioral sciences. Far from coercive, the authors frame the emerging perspectives from the 'third wave' of behavioral science as a view of humans firmly grounded in evolutionary anthropology and focused on our species' elaborated capacity for enlarging the scale of social cooperation through psychological flexibility in relation to identified values, at both the individual and small group levels of organization.

Part 2: Prosocial methods

This section builds on the theoretical perspectives from part one and offers more detailed insights and practical tools to engage real-world groups in reflective analysis and collaborative design of the social dynamics in their own groups.

Tools for psychological flexibility

The section begins by going into depth on the practical use of the *Prosocial Matrix* (Fig. 2), a tool for individuals and groups to notice and reflect on values and the behavioral variations that move us toward or away from these identified values. Importantly, this tool is grounded in foundational perspectives on the evolutionary origins of organismal behavior (see LeDoux 2019 for a current discussion from a congruent perspective), as well as the evolution of humans as a species with an elaborated capacity for symbolic verbal behaviors (Polk et al 2016). As the authors describe, "All animals will move toward food, warmth, and other experiences that sustain life and away from experiences of danger and pain that threaten life. Humans are no different in that respect, except that language and cognition make these toward and away processes much more complex" (Atkins et al. 2019, p. 74). The Prosocial Matrix is a tool that helps individuals and groups to reflect on their everyday experience in light of that complexity. The Prosocial Matrix is a tool that is in use in social-emotional learning programs in schools around the world, yet students are unlikely to get academic instruction on the evolution science that underpins this tool for cultivating psychological flexibility. As will be discussed in the final section of this review, whether evolution educators will agree on exactly how evolution science provides a scientific foundation for the Prosocial Matrix remains a very open question.

Evolving effective core design principles

Having outlined the basic toolkit for cultivating psychological flexibility, the authors take a deeper dive into each of the eight *Core Design Principles* generalized from the work of Elinor Ostrom. These sections include a wealth of interdisciplinary research in the human sciences that inform the relationship between the human universal aspects of the core design principles, and the expected cultural diversity found in communities around the world. This relationship between what may be universal to humans, and where healthy diversity can be expected in human behavior, cognition, and culture, is key to understanding the evolution of humans as an ultra-social primate. In this way, the explorations of each principle provide a well-rounded overview of key aspects of human behavior, cognition, and culture that have been important drivers over our phylogenetic history and are equally relevant for our everyday lives in modern society.

A better world is possible?

Some in the evolution education world may bristle at the notion of using evolutionary theory to strengthen

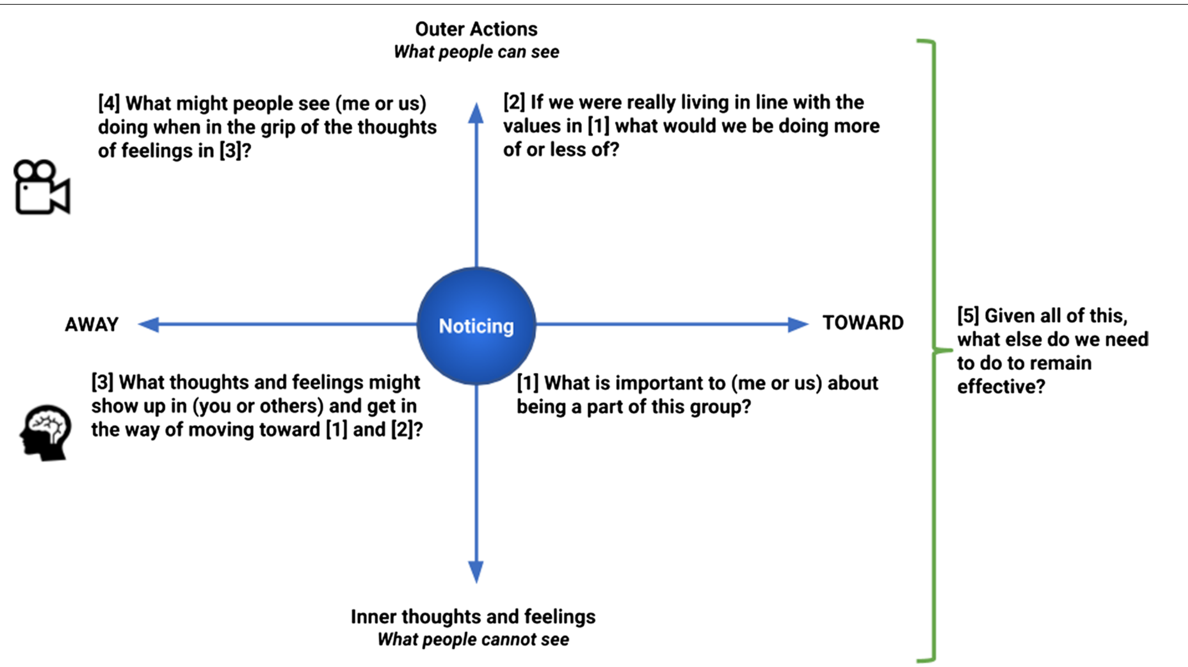

Fig. 2 The Prosocial Matrix is a practical tool for the cultivation of psychological flexibility, and is grounded in foundational perspectives on the evolutionary origins of organismal behavior at the most general level, and the evolutionary dynamics of humans as a species with elaborated symbolic verbal behavior more specifically

cooperation within and between communities, yet many may still appreciate the concluding call to action from the authors for moving towards "the more beautiful world our hearts know is possible" (Eisenstein 2013). Here, the authors sketch the future of the Prosocial research program and invite the readers to take an active role in using the science and practices outlined in the book to strengthen the communities we care most about. Whether evolution science ultimately can contribute making the world a better place is the question we argue evolution education should better engage with.

Considerations for evolution educators and education researchers

As Leigh Jr. (2019) points out in his review of David Sloan Wilson's other recent book, *This View of Life: Completing the Darwinian Revolution*, some of Wilson's language and claims regarding the causes and future of human cooperation may strike some readers as unhelpful or even incorrect. Leigh's criticisms are well founded, and indeed Wilson has a strong contingent of both supporters and detractors across evolutionary biology and the human sciences. Our point here is not to take sides for or against Wilson's view of evolution, simply to advocate that the existence of controversy at the level of respected scientific communities should not block the potential for productive discourse around the core conceptual claims as they pertain to evolution education. A full treatment of the educational implications of *Prosocial* is beyond the scope of this short review. Instead, we wish to highlight two questions we see as central to the value this work could offer educators and researchers in our field.

We argue that *Prosocial* opens questions that are currently under-addressed within evolution education discourse, and that working to engage current scientific discourse in these areas could strengthen the capacity to teach evolution as an interdisciplinary science relevant to the lives of students and school communities more globally. Specifically, engaging Prosocial within the evolution classroom requires addressing questions about the multilevel and multidimensional models of evolution utilized in this research program. Secondly, evolution education requires further clarification as to the appropriateness and the role of human behavior as subject matter within the evolution curriculum. Here, we do not intend to provide answers, rather only to frame questions for further exploration.

What is at the center of evolutionary analysis?

The multilevel and multidimensional view of evolution offered within Prosocial reflects a particular line of thinking steeped in historical debates about causation in biology and the relationship between biology, cognition, and culture in the causes of human behavior. Again, it is far beyond the scope of this article to resolve or even explore with any depth the nuances of this discourse, rather we aim to offer a frame for the potential value of deeper discussion within the evolution education community on these issues.

Prosocial frames a clear contrast between gene-centered individualistic views of evolution and the multilevel multidimensional model adopted by the authors. While these models remain the subject of debate among the evolution and human sciences, they are not fringe theories, and their relative prominence at the level of scientific discourse (c.f. Jabłonka and Lamb 2006; Uller and Laland 2019) compared with evolution education discourse (c.f. Deniz and Borgerding 2018) is worth noting. Put simply, these concepts reflect a significant scientific discourse in evolutionary biology and anthropology that is barely, if at all, engaged within the evolution education community.

The implications of this disconnect are not merely theoretical, but also practical. While it could seem reasonable to believe we should 'start with the basics' and therefore, "teach genetics first" (Mead et al. 2017), in fact the evidence is less than clear on this (c.f. Buchan et al. 2019), especially given the curriculum level directive to teach evolution early and often (c.f. Kelemen et al 2014; EvoKids 2015), and the science behind Prosocial may suggest other logical possibilities. Prosocial has been used in school professional development efforts in Australia, including among primary school educators adapting the core design principles into democratic classroom management tools for students. Such early work suggests the appropriateness of engaging students in reflecting on the behavioral and cultural variation that pervades their everyday lives, and provides a logical developmental pathway for conceptual understanding of more complex and evolutionary causal models of such everyday experiences. Our own efforts in international teacher development and curriculum design have offered early suggestions for Design-Based Implementation Research in this direction (Hanisch and Eirdosh 2019), but far more work is needed. Engaging the details of both conceptual clarification and teaching materials development will first require more clarity within the evolution education community on the role of human behavior as subject matter within the evolution curriculum.

Is human behavior a practical focus for evolution education?

Human behaviors, especially the kinds of social behaviors explored within Prosocial, are at the center of our everyday experience as humans, and have been key drivers of evolutionary change over our phylogenetic history. How students develop an understanding of the diversity of the human condition and our relative capacities of open-ended flexible adaptation to novel conditions is likely to be influential on their broader views of social organization and public policies affecting the sustainability of our species and the planet as we know it. The relevance of engaging students in scientific perspectives on human behavior is not so much in doubt, as much as there is simply a dearth of well-designed teaching tools or communities of practice focused on doing so within the context of evolution education (c.f. Eirdosh and Hanisch 2019; Hanisch and Eirdosh 2019). This is, in part, due to the complex historical, and current, sociology of scientific understandings or beliefs about the theoretical space for integrating evolutionary biology and human behavior (Wilson 2015). Prosocial situates itself within a very specific part of this theoretical space, as a knowledge synthesis project bridging evolutionary anthropology and multiple fields of applied behavioral sciences (Atkins et al. 2019). For some, this direction may appear highly problematic given the history of so-called "social darwinism" and popular conceptions of behavioral science as a tool of top-down or coercive control. In contrast, Prosocial is oriented around a reflection on human values from the individual to global levels and focuses on resolving potential conflicts between individual and collective interest at each level of organization. As Leigh Jr. (2019) points out, readers may view Wilson's core metaphor of a "multicellular society" as implying that individuals should become mere cogs in a larger machine, yet Prosocial makes clear that the intended transfer from this metaphor is the relative scope of lower level autonomy and higher level coordination around multiple spheres of shared interests. It is precisely this apparent conflict, between autonomy and coordination, individual and collective interests, that Prosocial provides tools for resolving and reflecting upon within a coherent body of evolutionary theory that is informed by current perspectives across the human sciences. For example, the notion that cooperation necessarily must come at the expense of individual interests and autonomy can be seen to imply a *zero-sum* mindset, rather than an understanding that social interactions can be, and for humans often are, *non-zero-sum* in nature (see e.g. Wright 2000), whereby the fate and interests of individuals in a group are aligned rather than opposed to each other. Against this view, the Wilsonian metaphor of a 'multicellular society' is about the need and potential to resolve these dialectical tensions rather than a suggestion to make individual interests wholly subservient to the society.

Conclusion

We suggest that while legitimate theoretical differences exist between gene-centered individualistic accounts of evolutionary change and the multilevel multidimensional accounts of Prosocial, the relevance to students' everyday lives and potential for productive clarification of core concepts in the evolution science curriculum indicate a strong potential for valuable engagement with these models of social change.

Prosocial is not a panacea for all the world's problems, but it does offer a range of practical tools grounded in a uniquely structured theoretical framework that aims to bridge current discourse in evolutionary biology and interdisciplinary human sciences. For this aim, the authors have done a laudable job at clearly communicating both the theory and practice of this applied research program. If and how the evolution education community can engage this work remains a very open question, yet we suggest there may be significant opportunity in doing so.

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The first author took the lead in the development of the manuscript, the second author provided substantive revisions and conceptual improvements. All authors read and approved the final manuscript.

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2.3 Contribution 3

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Eirdosh	50%	N/A	N/A	40%	N/A

Evolution: Education and Outreach

CURRICULUM AND EDUCATION

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Educational potential of teaching evolution as an interdisciplinary science

Susan Hanisch[1,2,3,4*] and Dustin Eirdosh[1,3,4]

Abstract

Evolution education continues to struggle with a range of persistent challenges spanning aspects of conceptual understanding, acceptance, and perceived relevance of evolutionary theory by students in general education. This article argues that a gene-centered conceptualization of evolution may inherently limit the degree to which these challenges can be effectively addressed, and may even precisely contribute to and exacerbate these challenges. Against that background, we also argue that a trait-centered, generalized, and interdisciplinary conceptualization of evolution may hold significant learning potential for advancing progress in addressing some of these persistent challenges facing evolution education. We outline a number of testable hypotheses about the educational value of teaching evolutionary theory from this more generalized and interdisciplinary conception.

Keywords: Conceptual understanding, Transfer of learning, Misconception, Gene-centrism, Systems thinking, Human evolution, Cultural evolution

Introduction

Evolutionary theory is continuously advancing and developing. New theoretical considerations based on new methods and empirical findings are being added over the years and decades into a more nuanced understanding of how evolution operates across the biological world and beyond.

Since Darwin's time, and especially in recent decades, scholars beyond traditionally biological fields have used concepts from evolutionary theory to explain observable variation and change of characteristics in populations–from economics, archeology, anthropology, sustainability science, linguistics, history, psychology, and computer science, to name just a few (see discussion in Hanisch and Eirdosh 2020a). While the history of extending evolution into the human domain is rife with scientific and ethical questions, many of these modern interdisciplinary developments in turn, have significantly helped to advance conceptual understanding of evolutionary theory, for example through the development of evolutionary game theory and agent-based modelling methods (Gintis 2009; McElreath and Boyd 2007; Rice 2004).

What all of these developments indicate is that evolution has become conceptualized more broadly as a *theory of change* that helps understand the variation and distribution of *heritable traits* of various kinds, rather than being restricted to rather gene-focused conceptualizations stemming from the so-called Modern Synthesis (MS).

What do these developments mean for how we teach evolution science, in biology, but also in other subject areas? Might these developments provide opportunities for advancing the understanding, acceptance or relevance of evolution, or might they in fact pose greater challenges for conceptual clarity in the future? Must these developments be actively incorporated to "keep up" with current science, or can these developments be safely put aside for various reasons?

These big picture questions frame the focus of our project, *Teaching evolution as an interdisciplinary science*, with the aim to encourage in the evolution education

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community (and other education communities) a wider discussion of these issues and propose a research program that explicitly explores these areas of educational potential.

In this article, we provide some perspectives and considerations in order to advance this aim, not least because, in our own educational initiatives, we have begun to actively incorporate aspects of evolutionary science from these broader and interdisciplinary perspectives. Importantly, our motivation to consider these broader conceptualizations of evolution for education is not merely driven by a concern for teaching current scientific discourse and nature of science. We argue that an understanding of evolution as it emerges from these interdisciplinary developments may help overcome some of the enduring learning difficulties in evolution education, and may provide more opportunities for interdisciplinary connections, both across biological subdisciplines as well as across the social sciences and humanities more broadly.

A general clarification of current evolutionary science is beyond the scope of this article. In Hanisch and Eirdosh (2020a), we provide such an overview of current evolutionary science discourse and a conceptual clarification of core concepts in evolutionary theory that highlights the generalization of concepts beyond gene-focused conceptualizations and beyond the domain of biology, as well as the broadening of evolutionary and developmental dynamics as more complex than commonly taught. We hypothesize that these generalizations of evolutionary concepts–while challenging the currently dominating gene-centered approaches to evolution education and assessment–may hold significant educational potential.

In Hanisch and Eirdosh (2020b), we discuss examples from evolution education discourse and materials that highlight how gene-focused conceptualizations prevail in standards, materials, and assessment tools, which may lead to inconsistencies, problematic representations of concepts, and problematic assessment items.

This article is structured as follows. In the following section, we summarize the persistent challenges of evolution understanding and acceptance that continue to prevail in evolution education. We then highlight areas of progress that have been made in terms of alleviating these challenges, as well as knowledge gaps and emerging opportunities for furthering this progress by employing an interdisciplinary, trait-centered conceptualization ofevolutionary theory. In the remainder of the article, we address each area of challenge in more detail, first regarding persistent barriers to evolution understanding, and then regarding persistent barriers to evolution acceptance, and provide hypotheses for how a generalized conception of evolutionary theory might help in further alleviating each area of challenge. In the concluding section, we point out existing and emerging teaching approaches designed to test our hypotheses, which we plan to explore in our design-based research project *Teaching evolution as an interdisciplinary science*.

Persistent challenges in evolution education

The evolution education community continues to be confronted with persistent challenges to evolution understanding and acceptance. One area of challenges pertains to the difficulty of understanding evolutionary concepts and principles due to conflicts with students' intuitive conceptions as well as the prevalence of common misconceptions and cognitive biases (Gregroy 2009; Pobiner 2016; Rosengren et al. 2012; Sinatra et al. 2008). Intuitive conceptions thought to hinder evolution understanding include the notion that individuals can adapt, that traits can be acquired during the lifetime and then transmitted to offspring and that natural selection is an event rather than a distributed process (Gregory 2009). Cognitive biases include essentialist views of organisms or groups of organisms such that variation between and within organisms that is important for natural selection is overlooked (e.g. Gelman 2003; Shtulman and Schulz 2008), teleological notions of causality that invoke a purpose, need, function, or goal (e.g. Barnes et al. 2017; Kelemen 2012), and similar intentionalist notions of causality that invoke an intentional agent (Gregory 2009; Varella 2018). Furthermore, due to some of these misconceptions and biases, the distributed, deep-time, multi-causal, multilevel nature of evolution and its emergent outcomes is difficult for students to understand (Chi et al. 2012; Cooper 2016; Jacobson 2001; Petrosino et al. 2015; Xu and Chi 2016).

Another area of challenge has to do with evolution acceptance due to emotional and motivational hurdles. One of those hurdles appears to be based on the perceived negative implications of evolutionary theory to personal life and society (e.g. Brem et al. 2003). For example, the notions of competition, extinction, and violence in nature might provoke in students a form of "existential anxiety" (Legare et al. 2018). Furthermore, a significant challenge is presented by the fact that evolutionary explanations of life, including the origins of humans, can conflict with religious beliefs and other factors of personal identity (e.g. Barnes et al. 2017; Bertka et al. 2019).

Note that there are complex interactions between challenges of understanding and acceptance, since emotional factors often cannot be separated from conceptual learning, and learning is understood by many scholars to involve affective and motivational aspects (Pugh 2011; Sinatra 2005). This is why evolution education has been particularly concerned with the apparent problem that understanding of evolution does not appear to coincide with acceptance, or motivation, or perceived relevance of evolution to students (Dunk et al. 2019; Pobiner 2016).

For example, Brem et al. (2003) investigated the perceived personal and social consequences of evolutionary theory among US undergraduate students in five potential areas of impact. Among other things, students (n = 135) were asked to rate to what degree they found evolutionary theory makes it harder or easier to justify selfishness or racial and ethnic discrimination, or whether evolutionary theory increases a sense of puropse and self-determination. Overwhelmingly, students held quite negative attitudes towards evolution regarding these notions. Furthermore, knowledge about evolution did not differ significantly between students across nine identified belief groups (from strong creationist to non-theistic evolutionist), and the extent of negative perceptions was strikingly similar across these belief groups. Authors conclude: "While we would hope that knowing more about evolution would lead to a richer understanding of complicated issues, these results suggest that the more a person knows about evolution, the more negative they become." (Brem et al. 2003, 194).

In the following section, we summarize some existing approaches and the progress that has been made to date towards addressing these persistent challenges. We then highlight knowledge gaps and emerging findings regarding the educational potential of an interdisciplinary evolutionary theory.

In the remainder of the article, we address each of these areas of difficulty and highlight how emerging interdisciplinary conceptions and applications of evolutionary theory might help make further progress on alleviating these challenges to effective evolution education.

Previous approaches and progress in resolving persistent challenges

While the challenges mentioned above continue to persist, it is important to emphasize that progress has also been made in the development of instructional strategies for addressing these.

For example, it has been shown that the mechanism of natural selection can be successfully taught to children as young as 5 years old through storybooks and activities (Brown et al. 2020; Emmons et al. 2016; Emmons et al. 2018; Kelemen et al. 2014; Shtulman et al. 2016). Brown et al. (2020) showed that while 7–9 year old students had predominant teleological explanations of the origins of traits, these could be significantly reduced by a short intervention in classroom settings. Importantly, in this context achieving an understanding of natural selection does not require an understanding of genetic variation and genetic inheritance (which presumably would be too abstract for young children). In contrast, other authors have argued that to increase understanding of evolution, teachers should "teach genetics prior to teaching evolution" (Mead et al. 2017).

Bruckermann et al. (2020) reviewed research into young children's understanding of important concepts of evolutionary theory, namely variation, inheritance, and natural selection, and effective interventions to use these conceptions as stepping stones, or conversely, to overcome them in order to develop a scientific understanding of evolution. Authors highlight that there might be complex interactions between children's intuitive understandings and biases that can hinder or foster understanding of natural selection. For example, educators might build on children's teleological notion that organisms respond to needs, as it can help them appreciate trait variation between organisms, or educators might build on children's early developing understanding of inheritance and essentialist biases to introduce rudimentary concepts of genetic inheritance.

Harms and Reiss (2019) summarize the successful teaching strategies for achieving student understanding and for addressing student attitudes towards evolutionary theory based on the chapters of their edited book. Pedagogical approaches that have been found to be effective in science education more broadly, have also been found to promote understanding and acceptance of evolution, including inquiry-based learning, use of models, games, and simulations, and using metacognitive strategies for students to explore their own conceptual change and understanding.

Several authors also found or proposed that the use of human examples, or examples that are closer to student everyday experience, can increase motivation and the perceived relevance of evolution (e.g. Pobiner et al. 2018; Nettle 2010), in turn affecting conceptual understanding.

Pugh et al. (2010) and Heddy and Sinatra (2013) built on the notion of transformative experience and its role in fostering conceptual change in their interventions with high school and undergraduate students. In these studies, instructional strategies that model or encourage the active use of concepts in everyday experience have been found to foster conceptual understanding and positive emotional affect in relation toevolution.

Deniz and Borgerding (2018) present the state of evolution education around the globe, including the degree of evolution acceptance across a range of countries. Evolution acceptance across countries ranges widely from about 80% in New Zealand, to about 60%–70% in countries like the UK and German-speaking countries, 50% in countries like US, Greece, and Ecuador, and 17% in Malaysia. Religion thus continues to present one of the most significant hurdles to the widespread teaching of evolutionary principles to the general public. To overcome this hurdle in the US context, Bertka et al. (2019) developed a teaching resource that was designed to help teachers and students to integrate religious beliefs with science in a more flexible and open fashion, in part by acknowledging and emphasizing that religious belief and science can coexist and be integrated. The interventions were rated positively by teachers and students across a range of religiosity.

Plutzer et al. (2020) found that between 2007 and 2019 the amount of time devoted to the teaching of human evolution and of evolutionary processes in the US has increased from an average of 4.1 to 7.7 h and 9.8 to 12.4 h, respectively. The percentage of teachers who convey evolutionary theory as established scientific fact also increased, and the percentage of teachers that consider evolution as a unifying theme in the biology classroom remained high and increased slightly to almost 70%. Identified factors that appear to be responsible for these improvements in the teaching of evolution are the adoption of the Next Generation Science Standards in the US as well as improvements in teacher and professional development.

Advancing progress by teaching evolution as a pluralistic and interdisciplinary science

Despite progress, there still exist significant knowledge gaps that might point to untapped potential for the evolution education world. Ziadie and Andrews (2018) conducted a review of research in evolution education to identify gaps in collective pedagogical content knowledge across themes in evolutionary theory. The authors found that, compared to the wealth of publications dealing with student thinking, assessment, and instructional strategies around the mechanism of natural selection, there are knowledge gaps regarding evolution of behavior and evolutionary developmental biology (no studies for high school level), coevolution, and sexual selection, particularly a lack of assessment tools for these concepts. Legare et al. (2018) point out that "[c]urrent 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." (p. 34). In this article, we argue that including more strongly the evolved nature of human cognition and behavior in evolution education may provide opportunities for tapping into student everyday experience and to increase students' perceived relevance of evolution, however, as Legare et al. (2018) note, this may require new approaches to assessing (and even defining) evolution understanding.

Nonetheless, some notable efforts exist to integrate a range of more complex notions and interdisciplinary examples of evolutionary change into high school and undergraduate evolution education. Thompson (2010) notes that the concept of coevolution should be more strongly emphasised in biology education. Thanukos (2010) highlights the educational potential provided by examples of coevolution in terms of student interest, the fact that examples of coevolution "can be used to illustrate key aspects of natural selection that students frequently miss" (p. 71), and the ability to integrate evolution concepts in the topic of ecology (thereby addressing the problem that evolution is still often covered as a separate topic in the curriculum, rather than as a theory that underlies and informs all other topics in biology, Nehm et al. 2009).

Love (2013) argued for an approach to evolution education that integrates the role of developmental processes and ecological interactions. Hiatt et al. (2013) surveyed US high school and university student conceptions of the developmental aspects of evolution (evo-devo), and found that students had difficulty integrating development and evolution. This may similarly stem from the aforementioned lack of integration of evolution with other topics in the high school biology curriculum (Nehm et al. 2009). Jamieson and Radick (2017) adapted a genetics course to tackle the issue of genetic determinism presumably stemming from an emphasis on Mendelian genetics, by putting a stronger emphasis on complex causes of phenotypes. Apodaca et al. (2019) included concepts like nongenetic inheritance, phenotypic plasticity, and niche construction in their concept map of evolutionary theory for biology education. However, as we note above, there is currently a lack of knowledge on student thinking and preconceptions, instructional strategies, and assessment tools available for teachers to explore these concepts in the classroom, particularly at the high school level (Ziadie and Andrews, 2018).

Araújo (2020) emphasizes the diversity and complexity in current evolutionary theory that should be embraced in order to more strongly establish the centrality of evolutionary theory in biology education, and criticizes the preponderance of gene-focused notions of evolution in education: "[E]evolution at both basic and higher education levels is strongly based on the original evolutionary synthesis [i.e. Modern Synthesis], with a focus on population genetics, and this is one of the reasons for the failure in establishing the centrality of evolution in biology teaching. Given the diversity and complexity of contemporary evolution theory, a more pluralistic perspective to evolutionary teaching is required. I propose that a causally pluralistic evolutionary worldview, which expands the range of causal factors contributing to evolutionary change, is essential when it comes to establishing the centrality of evolution in biology teaching." Araújo (2020, 1).

Wilson et al. (2019) explore and document the role of evolutionary theory in informing higher education curricula across a range of disciplines and topics. O'Brien et al. (2009), O'Brien and Gallup (2011), O'Brien and Wilson (2010), and Wilson (2005) present an interdisciplinary undergraduate evolution course ("Evolution for Everyone") that expands beyond the biological domain into the human sciences, includes topics such as cultural evolution, and applies evolutionary concepts to areas such economics and politics. As the authors lament, "evolution is still taught primarily as a subject in the biological sciences, rather than a theory that can help to unify the human-related disciplines." (O'Brien et al. 2009, 445), and "[t]here appear to be two walls of resistance, one denying the theory [of evolution] altogether and the other denying its relevance to human affairs." (Wilson 2005, 1001). O'Brien et al. (2009) found in a pre-post study that the course increased understanding and acceptance of evolution as well as perceived relevance to human-related disciplines and to everyday life. Wilson (2005) found a pronounced increase in student views about the relevance of evolution to human behavior, across religious and political background, as well as across a wide range of prior exposure to evolution. It would be interesting to know to what degree these outcomes of their course compare to more biology and gene-focused evolution courses, however, as Wilson (2005) notes, it is difficult to establish what an appropriate control would be.

Pugh et al. (2014) highlighted how the concept of natural selection is applied to various domains outside biology, such as economics, psychology, cognition and learning, and investigated high school students' ability to equally transfer the concept from biological examples to culture. The authors call for instructional approaches that make transfer an explicit goal and that help students to develop flexible representations of the concept of natural selection across domains. However, we are not aware of instructional strategies and their assessment for high school level that explicitly target this transfer of evolutionary concepts beyond the domain of biology.

In this article, we build on these emerging calls and approaches in evolution education towards a more generalized, interdisciplinary treatment of evolutionary theory across grade levels in general education. We propose thatthis approach has the potential to furtheradvance progress towards addressing the persistent challenges of evolution understanding and acceptance. To our knowledge, there is a dearth of empirical research or assessment tools to investigate this potential (see also the review by Ziadie & Andrews, 2018).

In fact, we argue that the teaching of evolution through a gene-centered conception might also inherently contribute to and exacerbate the persistent challenges in evolution education, thus constraining progress in addressing some of the challenges.

As we highlight further below, one set of reasons is that many intuitive understandings, such as the notion that individuals can adapt or that culture evolves, are considered misconceptions, or at best outside of the domain, under a gene-focused conceptualization of evolution. By contrast, under a more trait-centered, interdisciplinary conceptualization of evolution (see Hanisch and Eirdosh, 2020a), such notions might rather be considered scientifically adequate and integrated parts of explaining complex developmental and evolutionary dynamics. This might in turn serve as a stepping stone towards extending these concepts to the domain of genetic evolution.

Another set of reasons relates to the fact that a gene-centered conception of evolution limits the available examples of evolved and evolving phenomena that can be discussed in the classroom, thereby limiting the opportunities for far transfer and for fostering motivation and perceived relevance.

A gene-centered conception of evolution also tends to de-emphasize the complex, reciprocal and multilevel nature of causality in development and evolution, thereby limiting the degree to which evolution education can foster systems thinking.

Finally, a gene-centered conception of evolution may de-emphasize the active role of organisms in shaping evolutionary trajectories, thereby limiting the degree to which students' knowledge and experience of goal-directed behaviors can become an integrated part of evolutionary explanations (see Hanisch and Eirdosh 2020c).

These elements of a gene-focused conceptualization of evolution and contrasting framing within a trait-centered conceptualization (Fig. 1) are sometimes, but not always, antithetical to each other. More often than not, adopting a trait-centered approach requires only a nuanced difference in emphasis or enrichment of gene-centered approaches.

Figure 2 as well as Tables 1 and 3 provide an overview of our hypotheses regarding the potential to further advance progress in evolution education, which we expand upon in more detail in the following sections.

Addressing challenges of evolution understanding

Table 1 summarizes some of the persistent challenges in evolution education related to evolution understanding. We hypothesize that these challenges may be in part overcome in the following ways:

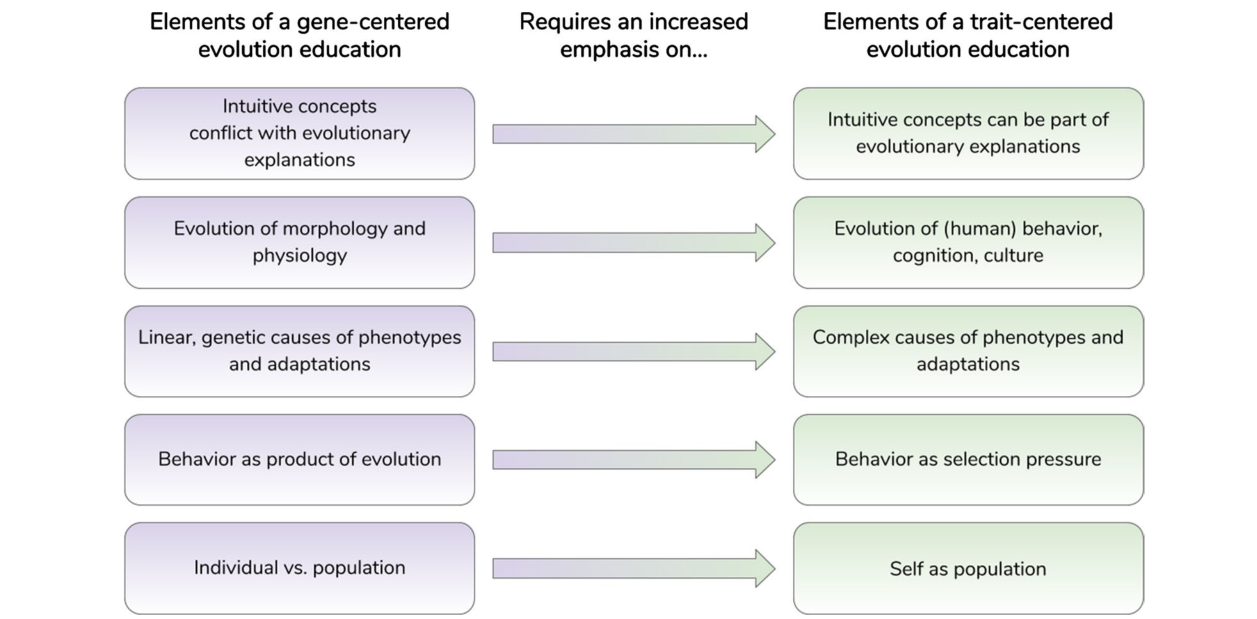

Fig. 1 Elements of a gene-centered evolution education compared with contrasting elements of a trait-centered approach

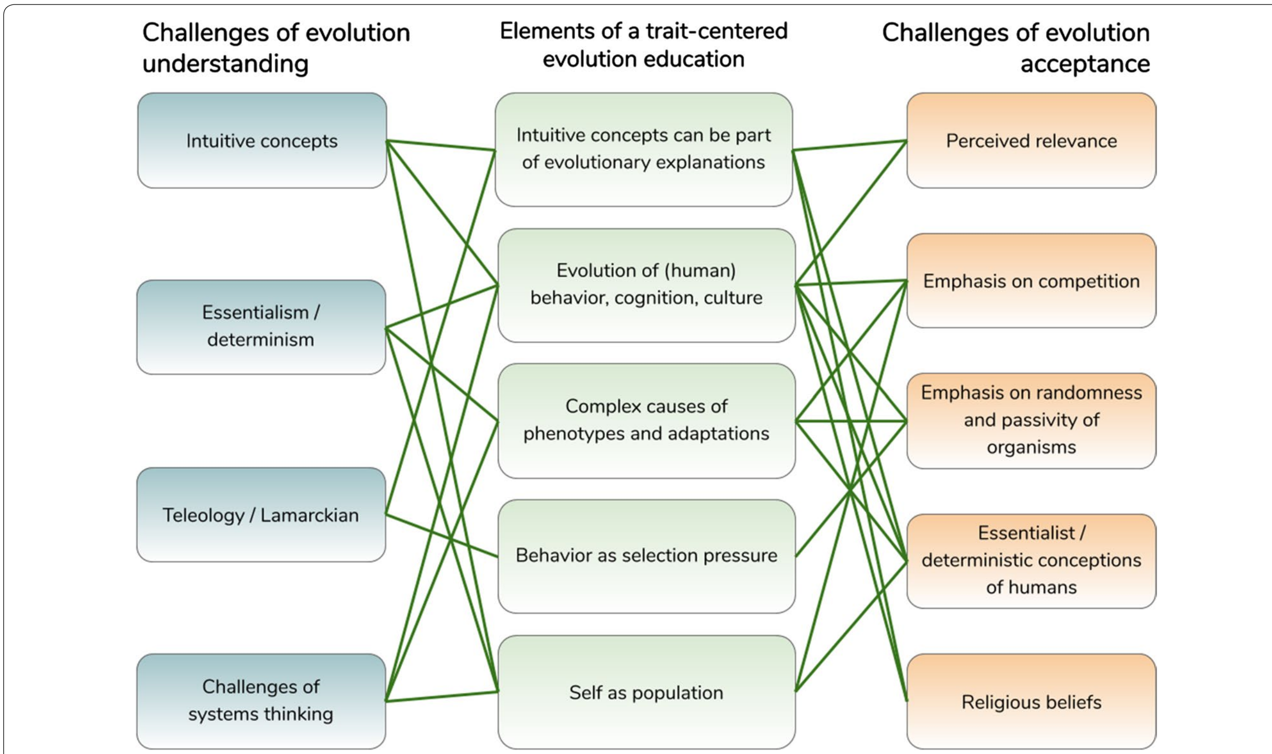

Fig. 2 Hypothesized pathways for addressing persistent challenges of evolution understanding and acceptance through greater emphasis of elements that are afforded by a trait-centered, interdisciplinary conceptualization of evolution. Lines in the figure highlight these pathways and hypotheses that are addressed in more detail in the text

Table 1 Persistent challenges to evolution understanding, with possible sources of the challenges stemming from a gene-focused conception of evolution, and hypothesised opportunities for overcoming these challenges afforded by an interdisciplinary conceptualization of evolution

Persistent challenges to evolution understanding	Possible sources of challenges stemming from a gene-focused conceptualization of evolution	Hypotheses for how teaching evolution as an interdisciplinary science may help make progress
Concepts of genetic evolution differ from intuitive, everyday concepts of the same name	Little explicit integration of students' intuitive understandings of concepts, e.g. that cultural traits and behaviors can be acquired and transmitted between individuals, that individuals change and adapt to circumstances during their lifetime	Generalized conceptions allow the integration of intuitive understandings explicitly as *bridges for transfer of learning*, e.g. through analogy maps for concepts such as inheritance, adaptation, information, individual, and population
Genetic determinism, essentialism	Emphasis of genetic variation as the primary (and sometimes only) form of variation considered relevant in evolutionary change, de-emphasis of the role of phenotypic variation, no explicit integration of cultural variation Emphasis of strong and direct genotype–phenotype relations Discouraging of students' intuitive understanding of changes on the level of the individual	A focus on phenotypic variation in humans, particularly regarding behavioral and cultural traits, can build on the saliency of human cultural variation Emphasis on complex interactions of many factors (beyond genes) and of learning impacting the developmental *reconstruction* of (behavioral, cognitive, cultural) phenotypes throughout life, e.g. through the use of causal maps Conception of the individual as an (evolving) population encourages defusion from an essentialist notion of the individual
Teleology, Lamarckian inheritance	Little explicit integration of students' intuitive understanding of the role of goal-directed behavior, other proximate mechanisms and ecological relationships in biology Emphasis on genetic inheritance as the only viable mechanism of inheritance	Explicit integration of behavior and other proximate mechanisms in evolutionary change, as well as explicit discussion of various variation-producing and transmission mechanisms on a trait by trait basis, beyond genetic variation and inheritance, develops the notion of complex causality of phenotypes, and allows the identification of problematic vs. unproblematic "teleological" and "Lamarckian" conceptions
Evolution entails complex interactions and emergent properties	A focus on genes as the primary (and sometimes only) sources of variation, and talk of "gene(s) for," strengthen the notion of "central agents" being in control A focus on selection as a unidirectional, linear process, and talk of "nature selects" at the expense of interactions and reciprocal causation, strengthen the notion of linearity and "selection as event" A focus on the individual as the primary (and sometimes only) level on which selection occurs, at expense of multilevel selection	Fostering a stronger incorporation of the concept of systems in evolution education by integrating interactions of many factors (environmental, social, organism traits, *plus* genes *involved in*….) beyond simplified gene-environment interactions, organism-environment interactions, or simplified genotype–phenotype relations, in evolving biological *systems*, e.g. through the use of causal maps, computer simulations and other teaching tools targeting systems thinking Using examples of current observable cultural evolutionary change to highlight complexity, such as the role of feedback loops in fashion trends, spread of innovations, and "viral" social media trends Integrate social structure and social interdependence and feedback between social environment and individuals Build on students' experience of the self as a complex and changing system or population

- Addressing misconceptions due to intuitive concepts by encouraging explicit transfer of learning from intuitive or observable phenomena to novel or more abstract phenomena, and explicit integration of intuitive understandings under a general conceptualization of evolution
- Addressing essentialism and genetic determinism by emphasising phenotypic variation and complex developmental reconstruction of phenotypes, including cultural phenotypes, as well as the notion of self as population or complex system
- Addressing teleological reasoning and Lamarckian inheritance by encouraging the explicit integration of behaviors as shaping selection pressure in evolutionary change, as well as student understanding of various mechanisms of inheritance into explanations of evolutionary change
- Addressing challenges related to complexity and systems thinking by emphasising complex causality in explanations of evolutionary and developmental change, exploring observable cultural evolutionary dynamics, and enhancing the notion of self as population or complex system.

Addressing misconceptions due to intuitive concepts through transfer of learning

Humans have an elaborated capacity for social cognition, inuitively noticing and interpreting the behavioral variation that pervades their everyday lives (Hermann et al. 2007; Heyes 2018). Evolution education has long recognized that students' intuitive concepts may pose challenges to scientifically adequate understanding of evolution science (see Shtulman 2017). Here we hypothesize that a trait-centered, generalized, and interdisciplinary conceptualization of evolution could help address this persistent challenge through fostering increased transfer of learning across relevant knowledge domains towards deeper conceptual understanding (sensu Stern et al. 2017).

Foundational to education science is the idea that all learning requires the transfer of prior learning to novel or more abstract phenomena (Kirschner and Hendrick 2020; Aubusson et al. 2006; Gentner et al. 2001; Haskell 2000). The role of analogical relations between prior concepts and novel experience in learning has led some cognitive scientists to argue that analogy is the "core of cognition" (Hofstadter 2001, 499). Despite the centrality of analogical transfer of learning to education, there remains a diversity of views as to how educators should practically engage this insight.

Kinchin (2000) contrasts a "systems view" of conceptual change with a "misconceptions" view. According to the misconceptions view, students' existing ideas "*interfere* with learning expert concepts" and teaching "must help pupils *replace* their misconceptions", whereas according to the systems view, "Pupils' *prior conceptions provide the only starting point* for instruction" and "Teaching should help the student *to appropriately extend* their prior knowledge." (Kinchin 2000, 180, emphasis original). Similarly in evolution education, it has been recognized that intuitive student conceptions may provide *bridges*, rather than barriers, which would allow students to transfer their understanding towards a more complex conceptual understanding (Evans and Rosengren 2018).

Opfer et al. (2012) also present considerations for designing evolution understanding assessment tools based on the cognitive foundations of learning and understanding, such as the role of core concepts that allow experts to organize and retrieve large stores of information, the role of causal relationships in expert explanations of phenomena, and the tendency of experts to increasingly generalize and abstract concepts and principles such that they can apply them across a range of different phenomena and even domains (i.e. far transfer, Barnett and Ceci 2002).

Pedagogical approaches for developing increasingly generalized and abstract representations of concepts that promote transfer of learning include the use of analogies and case comparisons (Alfieri et al. 2013) and the construction of analogy maps, whereby source and target phenomena can be compared by underlying common principles, processes, and other "deep" characteristics, thus developing the skill to transfer understanding to novel phenomena that may, on the surface, appear very different or involve different substrates and context-specific mechanisms (Gentner et al. 2004; Glynn 2008; Harrison and Treagust 2006). Goldstone and Wilensky (2003) provide evidence about the potential of computer simulations of various concreteness and abstraction to promote increasing generalization and transfer of principles of complex adaptive systems. Evolution educators have pointed out the need to assess student understanding of evolutionary concepts across a range of context examples, such as covering familiar and unfamiliar traits as well as a range of taxa (Nehm et al. 2010, 2012; Opfer et al.2 012). Emmons et al. (2018) investigated 6 and8 year old children's ability to transfer the concept of natural selection between scenarios involving similar traits (which they classify as near transfer) and dissimilar traits (which they classify as far transfer) and after a 1 month delay with the help of story books and guided classroom discussions. Kindergartners were able to transfer to similar scenarios but had trouble transferring to a more dissimilar context, while 8 year olds were able to transfer near and far to the same degree.

Barnett and Ceci (2002) highlight how definitions of near and far transfer vary widely across studies, and propose a taxonomy of far transfer. According to Barnett and Ceci (2002), transfer can be considered near or far along several dimensions: the similarity in knowledge domain (e.g. biology vs. economics), modality (e.g. text vs. images), and physical, temporal, functional and social context.

For example, according to the classification by Barnett and Ceci (2002), exploring and fostering students' ability to apply the logic of natural selection to different traits or species would be an instance of near transfer because it is in the same knowledge domain of biology, but might be considered far transfer if the context is presented in a different modality (e.g. text and pictures) or presented weeks or years later, or if it is set in a different context than the classroom or academic setting. As such, the different aspects of transfer studied by Emmons et al. (2018) highlighted above, while able to detect an important shift between 6- and 8-year olds' ability to transfer to increasingly dissimilar contexts and after a 1 month time lag, may all still be considered near transfer on a number of dimensions, particularly the domain (all examples are animals) and the physical and functional context (all testing was done in the school and was an academic activity). Assessment tools for natural selection for secondary and undergraduate students, while often using a range of context examples, similarly do not seem to capitalize on maximizing far transfer in the dimensions of domain (examples are within the domain of biology, and often more restricted still, involve animal morphological and physiological traits) and functional contexts (academic vs. applied to everyday life) (e.g. Anderson et al. 2002; Kalinowski et al. 2016; Nehm et al. 2012).

We argue that a trait-centered interdisciplinary evolutionary theory can further advance evolution understanding based on the role of far transfer in conceptual understanding.

On the one hand, transfer of evolutionary concepts and methods has been foundational to the application of evolutionary theory to other domains beyond biology (e.g. Lake and Venti 2009; Levinson and Gray 2012; MacCallum et al. 2012; Prentiss et al. 2011; Sweller and Sweller 2006). For example, cultural evolution science studies the changes of cultural variation in populations (of humans but also other animals) over time, using concepts and methods that have originally beendeveloped within evolutionary biology, such as modelling of population dynamics and phylogenetic analysis as well as comparative behavioral observations and experiments (Cultural Evolution Science 2020; Mesoudi, 2011). In this regard, variations of analogy maps and similar conceptual clarifications have been put forward by evolutionary scientists that compare processes and principles across different formulations or domains of evolutionary theory (e.g. Mesoudi 2011; Laland et al. 2015; Sweller and Sweller 2006). We draw on these in our conceptual clarification of evolution as an interdisciplinary science (Hanish and Eirdosh 2020a) as well as Table 2.

Thus, the application of evolutionary theory to the domain of culture arguably represents an opportunity to develop in students an even deeper and more abstract conceptual understanding of concepts of variation, inheritance/transmission, and selection (as well as other evolutionary processes such as drift) as can be achieved by focusing on biological examples alone. In order to investigate this potential, Pugh et al. (2014) explored 9th and 10th grade high school students' ability to transfer the concept of natural selection to the domain of culture by asking "Not only do organisms change over time, but so do [TV programmes/shoes]. In what ways, if any, is this change similar to evolution of organisms through natural selection? In what ways, if any, is it different?" (p. 26). Students' ability to correctly transfer the concept of natural selection to TV shows and shoes was rather small–26% showed no transfer at all, and more than half of students

Table 2 Analogy table comparing genetic evolution and cultural evolution as well as individual-level learning by general evolutionary concepts of variation, selection, and inheritance of traits. For an extended table and references, see Hanisch and Eirdosh (2020a, Table 1)

Concept, process, principle	Genetic evolution	Cultural evolution	Learning
How is variation of traits caused?	Mutation, recombination	Creativity, innovations, recombination of ideas, mistakes, reactions to new environments	Creativity, innovations, social learning, recombination of ideas, mistakes, reactions to new environments
How does selection of traits occur?	Higher chances of survival and reproduction compared to other trait variants	Higher chances of survival and reproduction (*natural selection*); higher appeal or attractiveness of the trait (*cultural selection*)	Success in achieving a goal
How are traits inherited, transmitted, or retained?	Biological reproduction, mitosis/meiosis	Social learning/imitation, teaching; technologies and infrastructure that endure	Reinforcement, encoding of neural connections in the brain

only provided answers coded as surface level transfer such as using phrases like "TV shows adapt" without further explication, while 28% showed some deep structure transfer that described the process of natural selection, using concepts like variation and survival of the fittest. These numbers dropped further at a 5-week follow up test. Importantly, students that showed higher levels of *deep structure* transfer also tended to show higher levels of conceptual understanding of natural selection, whereas there was no correlation between conceptual understanding and surface-level transfer. However, in this study, students were not explicitly instructed about the goal of transfer, or about the exact way that natural selection can be transferred across domains. This may be one reason that the relation between student conceptual understanding and ability for deep transfer was still rather small. Nonetheless, it seems promising that more than a quarter of students were able to transfer their understanding of biological natural selection to the domain of culture on a deeper level at all. Authors conclude that "We propose that for students to successfully transfer the concept of natural selection, they need to develop a particular set of cognitive structures related to the concept. Such cognitive structures include, but are not limited to, multiple representations of the concept (…), connections between the concept and multiple contexts and purposes (…), and conditional knowledge about how, when, where and how to apply the concept." (p. 31). Instructional strategies suggested by Pugh et al. (2014) include the exploration of various components of natural selection across multiple cases within and outside of biology, use of analogies, and explicit framing of the purpose of learning as transferring and applying a concept generatively to novel contexts.

Towards this aim, Table 2 provides an example analogy map we have used to engage pre-service educators from multiple subject areas in identifying and discussing the surficial difference and deeper structural similarities between genetic and cultural evolution in populations, as well as learning in individuals, along the three overarching concepts of variation, selection and inheritance/transmission/retention that are involved in the process of natural selection (see Additional file 1 for a lesson plan on exploring cultural evolution further). Note that the transfer of evolutionary processes to learning at the level of the individual represents an opportunity to link to and appropriately expand students' notion that individuals can adapt (see further below).

Another educational opportunity to promote conceptual understanding of evolution through far transfer may be due to the fact that concepts such as variation, inheritance, and selection as they are understood within cultural evolution science (see Hanisch and Eirdosh 2020a; Table 2), could often be considered closer to students' everyday experience and thus intuitive notions of these concepts, compared to the exclusively gene-centered understandings.

For example, regarding the ability to notice variation, Shtulman and Schulz (2008) found that more children and adults regarded behavioral traits as potentially and actually variable among individuals of a species compared to external or internal anatomical traits.

Regarding intuitive notions of inheritance, studies have shown that human folk biological and folk sociological intuitions across cultures also appear to be in line with the conceptualization of trait transmission through multiple possible mechanisms. Moya et al. (2015) assessed causal reasoning across cultures (US, Fiji, Peru) and ages (childhood to > 70 years) about transmission of different kinds of traits, namely morphological traits vs. cultural traits such as beliefs and skills, through "switched at birth" vignettes. Results showed that, while younger children tended to be biased towards thinking that all traits are inherited from biological parents, by middle childhood, subjects across cultures tended to reason that morphological traits are more likely to be inherited from biological parents before birth, and that beliefs (a type of cultural trait) are more likely to be inherited through social transmission from others in the social environment. Authors attribute this ability to differentiate between mechanisms of transmission to a mix of folk biology and folk sociology in humans across cultures. Similar studies equally indicate that "young children have a theory of kinship that allows them to differentiate biological inheritance and cultural transmission" (Duncan et al. 2009, 664; Venville et al. 2005).

In this view, it could be hypothesized that engaging students in understanding the variability, transmission mechanisms, and context-specific functional consequences of behavioral or cultural traits couldrepresent an important "stepping stone" (sensu Evans and Rosengren 2018) towards understanding gene-centered concepts in biology, which are known to be difficult for students to grasp (Duncan et al. 2009).

Further still, student ideas of behavioral and cultural change might in fact be considered *part of* a scientifically adequate evolutionary account, particularly regarding cultural and gene-culture coevolutionary dynamics and the role of behavior-led adaptation and niche construction (e.g. Henrich 2016; Laland et al. 2011; Odling-Smee et al. 2003; Richerson and Boyd 2005). Opportunities for far transfer to different physical and functional contexts outside the classroom thus present themselves because students experience a wide range of cultural evolutionary phenomena in their everyday lives, which has implications for student motivation and perceived relevance of evolution (see below). As Prentiss et al. (2011) point out in their presentation of the evolution of skateboard designs by employing evolutionary concepts and methods, "our familiarity with changes in modern material culture provide an excellent opportunity for teachers to utilize material culture evolution to inform larger discussions of evolution in general". This view is in contrast to how some evolution education scholars appear to make a hard distinction between evolution as applied to culture and evolution as used in the domain of biology (e.g. van Dijk and Reydon, 2010; see Hanisch and Eirdosh 2020b for a discussion), rather than integrating them into a higher level causal model of evolutionary change. In fact, cultural evolution is already part of the biology education curriculum in Germany, and in Hanisch and Eirdosh (2020b) we document how some German biology textbooks (as well as primary school education materials, Graf and Schmidt-Salomon 2017), make explicit the analogical nature between genetic and cultural evolution, but in our view, do not provide sufficient guidance to students and teachers to think more carefully about the structural similarities and differences between biological and cultural evolution.

Stepping from more intuitive to less intuitive understandings requires carefully structured scaffolding towards generalized understanding of core concepts that can be flexibly and appropriately transferred into specific contexts (Stern et al. 2017; Vendetti et al. 2015). Thus, from the "conceptual ecologies" (Kinchin 2000) and teaching for conceptual understanding perspectives (Stern et al. 2017), in order to help students to develop a deeper, transferable understanding of concepts like, for example, "inheritance", we can encourage them to reflect a little deeper on, enrich and complexify their current existing understanding of this concept by prompting them with specific reflection questions such as: How would you define it? What characterizes it? What are some examples of things that can be inherited or passed on between organisms? Through what ways or processes can things be inherited or passed on to others? Who can inherit what from whom and to whom? With some prompting, students' existing "conceptual ecologies" related to inheritance can be elaborated to a broad understanding that organisms inherit, pass on or transmit various things and characteristics to other organisms through various mechanisms. With the explicit construction of analogy maps, the concept of inheritance can serve as an overarching *causal process* involved in evolutionary change, and genetic inheritance can become one particular *kind of inheritance*, whereby the differences between other kinds of inheritance are compared in terms of the specific details of certain aspects and mechanisms, such as the kinds of things that are inherited (e.g. genes vs. behaviors vs. technologies vs. money), how they are inherited (e.g. biological reproduction vs. imitation vs. persistence vs. by social norms and laws), or to whom in a group they can be inherited (e.g. vertically between parents and offspring, or horizontally and obliquely).

Similar approaches for building on students' existing, but often unreflected and rudimentary, knowledge of everyday terms are thinkable for almost all the concepts that are central to evolutionary theory (see Hanisch and Eirdosh 2020a), including "adaptation", "natural selection" (see Pugh et al. 2014) and the term "evolution" itself. Such potential for transfer may also help foster connections across topics in the biology curriculum, as well as interdisciplinary connections across school subjects, and may have implications regarding motivational hurdles, e.g. by promoting relevance of evolution to student lives.

Addressing essentialism and genetic determinism

Essentialism is a cognitive bias whereby students tend to not see the variation among individuals of a population or species, often ascribing to them a certain unchangeable essence (Gelman 2003; Pobiner 2016). Such essentialist biases stand in the way of a conceptual understanding of evolution by natural selection, which requires population thinking and an appreciation of the role of variation (Shtulman 2006).

Genetic determinism is a cognitive bias or misconception whereby students tend to expect that phenotypes are solely and directly determined by genes and not at all or barely influenced by other factors (Jamieson and Radick 2017).

We argue that an emphasis on genetic variation as the primary (and sometimes only) form of variation that is relevant in evolutionary change and in the development of phenotypes may reinforce essentialism and genetic determinism by de-emphasizing the role of phenotypic variation.

Standards and textbooks tend to emphasize simple and direct genotype–phenotype relations, sometimes using genotype and phenotype seemingly interchangeably (e.g. University of California Museum of Paleontology, 2009; see Hanisch and Eirdosh 2020b for more examples and discussion). This may reinforce genetic determinism by de-emphasizing the role of developmental *reconstruction* (sensu Oyama et al. 2001; see Hanisch and Eirdosh 2020a, c) of phenotypes, whereby phenotypes develop by the integration of a variety of heritable resources and factors, including but not limited to genes. Oyama et al. (2001) argue that conceptions of evolution and development that only regard genetic information as determining phenotype and as relevant in shaping evolutionary trajectories are merely an extension of earlier preformationist notions that held that organisms are in some way preformed in the embryo, rather than more appropriate epigenetic notions that consider development as a process of complex causality involving many sources of information. Similarly, an emphasis on a direct genotype–phenotype relation in the classroom can be regarded as problematic, since the notion of an immutable "essence" of organisms that is considered part of essentialist biases is simply replaced (and possibly even reinforced) by the concept of genes. Indeed, Ergazaki et al. (2015) introduced the concept of "species-genes" and "body-trait-genes" to provide 5-year old children with a rudimentary biological explanation of the mechanism that explains species and trait-resemblance between parents and offspring. The intervention increased children's understanding of biological inheritance and decreased their endorsement for the causal role of parents' wishes and intentions in influencing their offsprings' species and body traits. However, the danger might be that an "essence-like idea of genes" (Eragazi et al. 2015, 3136) reinforces essentialist notions of an immutable essence of species and individuals. As Bruckermann et al. (2020) highlight, there may be complex interactions and trade-offs between building on children's intuitive notions of teleology and essentialism towards an understanding of evolution.

Genetic determinism may also be further reinforced if educators regard as deterministic the notion that one gene determines one trait, seaking to overcome such notions with an emphasis that many genes are involved in a phenotype, or that it is the proteins produced in the expression of these genes that lead to phenotypes (e.g. Duncan et al. 2009). Hanisch and Eirdosh (2020b) document examples of problematic educational materials potentially reinforcing, explicitly or implicitly, notions of genetic determinism.

In contrast, Jamieson and Radick (2017) adapted an undergraduate genetics course to tackle the issue of genetic determinism presumably stemming from an emphasis onMendelian genetics. They sought to emphasize the role of developmental factors such as behaviors and environment in the emergence of a focal phenotype by the use of causal maps, and to deemphasize language like "gene for", replacing it with "gene(s) involved in". The authors pointed out that 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." (Jamieson and Radick 2017, 1268). We argue that the approach of "leading with complexity" (Fuentes 2020), can also be applied to evolution education and may help overcome a range of challenges of evolution understanding, as well as emotional and motivational hurdles (see below). Figure 3 visualizes the different notions of phenotype causation characteristic of a gene-centered and trait-focused understanding of evolution.

It has been argued that teaching about evolutionary concepts like variation through human examples can have positive impacts on student understanding, because variation in our species appears to be more salient to students (Nettle 2010). However, within a gene-focused conceptualization of evolution, the particularly striking behavioral and cultural variation in our species can not be integrated as relevant or appropriate forms of variation for gene-centered evolutionary explanations. Under the generalized notion of evolution within cultural evolution science, however, cultural phenotypes can become valid phenomena whose change and distribution can be investigated through the mechanisms of variation, selection and transmission (as well as other processes; see the previous section, Table 2, Additional file 1, and Hanisch and Eirdosh, 2020a). Further still, such cultural variation can act as selection pressures driving evolutionary change at the genetic level, as is the case in the expanding set of documented instances of culture driven gene-culture co-evolution, such as the evolution of lactose tolerance and other adaptations to agricultural practices, behavioral adaptations to socio-cultural environments, immunity to pathogens, the evolution of language, and the concept of self-domestication (e.g. Chudek and Henrich 2011; Hare et al. 2012; Jablonka et al. 2012; Laland et al. 2010). While the social and constructed environment, combined with social learning, shape behavioral traits across a wide range of animals (Hoppitt and Laland 2013; Odling-Smee et al. 2003; Whiten and van Schaik 2007), these dynamics are especially pronounced in our own species, where the socio-cultural environment has a prominent role in influencing our behavior and cognition throughout development.

Similarly, under a gene-focused conceptualization of evolution, students' intuitive understanding that individuals change and adapt throughout life in interaction with their environment is usually discouraged, being framed as an inaccurate use of the term adaptation (i.e. individuals don't adapt, only populations do). This may reinforce essentialist and deterministic notions. Instead, under a generalized conceptualization of evolution, the concept of the individual can be explicitly transferred to the concept of an (evolving) population, changing through the mechanisms of variation and selective retention in the case of learning and behavioral change (see Table 2; Hanisch and Eirdosh 2020a). As Shtulman (2006) highlights "science educators should be aware that their students are likely to analogize the adaptation of species to the adaptation of individuals, (…). One strategy for ridding students of such essence-based analogies would be to contrast them with population-based analogies" (p.

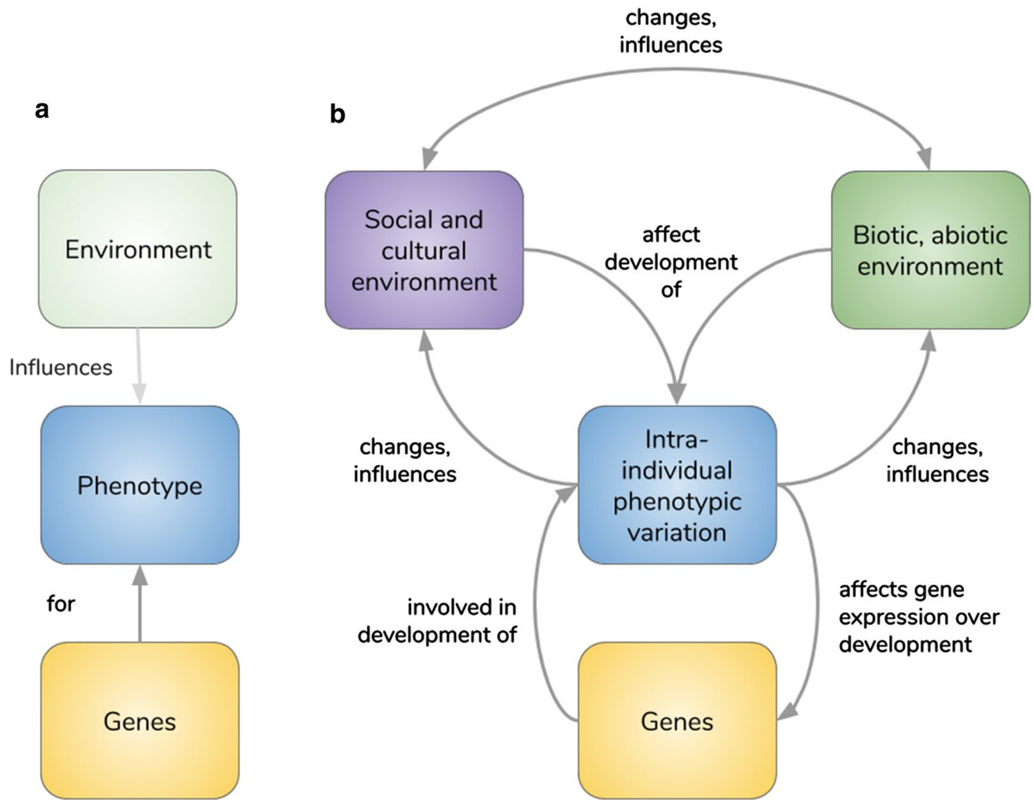

Fig. 3 Different representations of the causes of phenotypes. **a** Emphasis on linear and direct genotype–phenotype relations, sometimes with a footnote about the role of environment, that characterizes gene-focused notions about the causes of phenotypes. **b** Multi-causal and reciprocal interactions shaping intra individual phenotypic variation throughout development, as conceptualized in trait-centered and generalised evolution science. Note that in this case, various inheritance streams, beyond genetic inheritance, can become relevant in the reconstruction of phenotypes, and hence in the evolution of adaptations. Sources: Laland et al. (2011); Oyama et al. (2001); Jamieson and Radick (2017)

186). Thus, the question is whether population-based analogies *could* appropriately be applied to the level of individuals, which could then be conceptualized to adapt and evolve by population-level evolutionary processes. In fact, this is what scientists across a range of disciplines have done, including in cancer research, psychology, and cognition, as well as in evolutionary biology towards explaining the evolution of multicellularity (e.g. Aktipis 2016; Greaves 2018; Hayes and Sanford 2015; Rosenbaum, 2014; Smith and Szathmáry 1995). Thus, evolutionary processes are being recognized among many scientists to operate across multiple scales of time and levels of organization, allowing for an enrichment rather than correction of students' intuitive conceptions of individual-level adaptive change. However, as we highlighted above, this requires careful scaffolding and instructional design to help students *transfer appropriately* between the processes involved in the adaptation on the level of individuals and adaptation on the level of populations of individuals (see Table 2). Indeed, we recognize that many in the evolution education community remain reluctant to accept the conceptualization of individual organisms as evolving populations of cells and traits, however, at the level of evolutionary science this concept has a long history, remaining significant in current discourse. In light of the educational aim of teaching for conceptual clarity, we argue this learning potential should be on the research agenda for evolution education.

Addressing challenges of teleological reasoning and Lamarckian inheritance

Challenges of evolution understanding also revolve around a class of misconceptions that have been termed teleological thinking, and a similar class of misconceptions that have been termed "Lamarckian" thinking.

Teleology is defined in different ways by educators, but often it is described as involving a reference to purpose, need or function in causal explanations of phenomena (e.g. Brown et al. 2020; Kelemen 2012). At the same time, students' reference to need has also been considered to be an appropriate bridge or scaffolding towards an understanding of natural selection because of the recognition of the role of trait function (Evans and Rosengren 2018; Legare et al. 2013). Similarly, it has been pointed out that student thinking about causality in biology may not be an invalid "teleological" notion but a valid account of proximate and ecological interactions, or an implicit understanding about the role of antecedent causes in bringing about functional traits (e.g. Gouvea and Simon 2018; Ojalehto et al. 2013; see Hanisch and Eirdosh 2020c, for an extended discussion).

Similar problems apply to Lamarckian thinking, where it has been pointed out that educators also define Lamarckian conceptions differently, and different student conceptions may be falsely categorized as "Lamarckian" (Kampourakis and Zogza 2007). Broadly, Lamarckian type reasoning in causal explanations of traits involve notions that the use or disuse of organs or body parts leads to heritable changes to organism morphology over generations (Kampourakis and Zogza 2007).

Prevalence of teleological reasoning in children when it comes to explaining changes in organism traits over time, can be overcome with short interventions that target population thinking (e.g. Brown et al. 2020; Emmon et al. 2016). Despite this, educators lament that teleological language appears to prevail among older students and adults (e.g. Barnes et al. 2017; Coley and Tanner 2015; Kelemen and Rosset 2009).

We argue that the challenges related to overcoming these misconceptions, as well as to interpreting student ideas as appropriate vs. inappropriate causal accounts, may stem from the issue that, in gene-centered conceptualizations of evolution, proximate mechanisms (including behavioral variation, behavioral responses to perceived needs, learning, ecological relationships, developmental factors, and reciprocal causation) are de-emphasized in explanations of evolutionary change or of the origins of adaptations. Furthermore, the problem with seemingly Lamarckian-type inheritance or teleological conceptualizations may stem from the fact that inheritance streams beyond genetic inheritance–which people across ages and cultures appear to have an intuitive understanding of (see Moya et al. 2015, and Venville et al. 2005 cited above; Andrews et al. 2011 cited below)–are not being sufficiently elaborated on in the classroom as part of evolutionary explanations and, often, drivers of evolutionary change.

Misconceptions such as teleological reasoning or the notion that traits acquired during development can be passed on to offspring, may be difficult to overcome because it is difficult to "extinguish" or completely replace students' everyday experience of behaviors and needs, their observations of goal-directed behaviors of animals, and their observations that–at least in the human realm–we acquire and transmit many (cognitive, behavioral, and cultural) traits in our lifetime. As Legare and Shtulman (2018) and Chi et al. (2012) point out, different and sometimes seemingly logically inconsistent conceptualizations and schemas may often coexist and be activated for different purposes and in different contexts, including contexts for which these schemas may not be appropriate. Legare and Shtulman (2018) propose that one way to reconcilecoexisting schemas that seem to be inconsistent is to integrate them into a larger causal structure, and they call for research in science education around methods and factors that "promote the construction of integrated, yet scientifically accurate, explanatory models".

In this regard, it is interesting that in the study by Brown et al. (2020), primary school students that held "explicit" teleological notions had higher factual biological knowledge than students that held ambiguous misconceptions. Thus, it seems that the more students learn about a diversity of biological facts throughout development, they need opportunities and supports to integrate their valid conceptions about biology, including about behavioral biology and other proximate causes operating during development, with an account of how such proximate causes combine with genetic inheritance and natural selection to produce adaptations over phylogeny.

Gene-focused conceptualizations of evolution may, currently, not sufficiently support this integration. 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 idealization may help in understanding broader phylogenetic changes across a range of phenomena, but they may provide rather limited understanding if the interest is in a more concrete account of the role of developmental processes and other proximate mechanisms in explaining particular phenomena. As we also point out in Hanisch and Eirdosh (2020a), we suspect that such idealizations may also wrongfully lead educators to the conclusion that the (idealized, abstracted) conceptualizations of evolution within the framework of the MS represent a more fundamental *truth -* such that processes operating in development have no causal role in evolutionary change, and student reasoning that references such processes is considered a misconception.

Conversely, generalized conceptions of evolutionary dynamics include and integrate explicitly the roles of developmental factors and proximate mechanisms in bringing about evolutionary change (e.g. Laland et al. 2015; see Hanisch and Eirdosh 2020a). This provides students with opportunities to link their understanding and experiences of proximate mechanisms with evolutionary change. For example, student reasoning that animals respond to needs with behavior, can be productively included in causal explanations of evolutionary change through an understanding of the role of behavior as selection pressure or by introducing the concept of niche construction (Mayr 1970; Odlings-Smee et al. 2003). In Hanisch and Eirdosh (2020c), we present a causal mapping teaching tool that allows this integration of proximate and ultimate mechanisms when exploring the causation of behavioral, cognitive, socio-cultural, morphological, and physiological traits during human evolution in secondary school classrooms.

Generalized conceptions of evolutionary dynamics also include and integrate a range of inheritance streams and mechanisms, beyond genetic inheritance (Jablonka and Lamb 2005). This is particularly relevant to the apparent student misconception that acquired traits can be inherited. We argue that discussing the appropriate inheritance mechanisms on a trait by trait basis can help distinguish between correct and incorrect notions about the possible inheritance of acquired traits (see Table 2, Additional file 1). Particularly, novel behavioral traits may well be acquired by animals during their development in response to environmental conditions (called environmental induction, Laland et al. 2015), and those behaviors may in turn be transmitted to offspring as well as others in the population through social learning. Conversely, morphological features that have a strong genetic basis can not be acquired during development and can only be passed on to offspring through genetic inheritance. Many phenotypic traits will develop through complex interactions between various variation producing processes and inheritance mechanisms, including through epigenetic and ecological inheritance (see Hanisch and Eirdosh 2020a).

Addressing challenges of systems thinking

Evolution educators lament that students have difficulty understanding the complexity and multilevel nature of evolutionary change (Chi et al. 2012; Cooper 2016; Jacobson 2001; Petrosino et al. 2015). Elements of systems thinking include seeing multiple causes rather than single causes, understanding that small causes can have big effects (through delays and non-linear rather than linear cause-effect relationships), understanding that system dynamics result from interactions between elements in the system rather than through central control, and explaining phenomena through emergence rather than through the additive effects of isolated parts (Jacobson 2001; Perkins and Grotzer 2005).

The system concept is often a core concept in biology education standards (e.g. in the Next Generation Science Standards, Achieve 2013). However, our hypothesis is that, while the concept of system may be emphasised in the topics of ecology or physiology in the biology curriculum, in the realm of evolution, an emphasis on genes, on a unidirectional account of selection (from the environment to the organism or to genes), on a centralized notion of "nature selects" (Gregory 2009), as well as on a linear and direct relation between genotype and phenotype may rather stand in the way of applying the concept of system and the complex causality in such systems, to evolution understanding (see Hanisch and Eirdosh 2020b for examples in evolution education standards and materials).

In contrast, generalized and trait-focused conceptualizations of evolution (and development) promote a decentralized view of evolving biological systems, informed by concepts and methods of systems biology and complexity science, by explicitly integrating complex proximate and ecological interactions in evolutionary change. An integration of various interacting factors as causes of phenotypic reconstruction over the course of development, with genes being one type of cause *involved in* phenotypes, can foster an important aspect of systems thinking (i.e. multiple and reciprocal causality, see Fig. 3).

Furthermore, the ability to use examples of current observable *cultural* evolutionary change under a more generalized conception of evolution, can serve to highlight complex systems dynamics observable in students' lives, such as the role of feedback loops in fashion trends, the spread of innovations, and "viral" social mediatrends, thus providing opportunities for fostering far transfer of evolutionary dynamics between different domains.

An emphasis on the individual as the primary (and sometimes only) level on which selection occurs, as well as a rather simplified notion of population, abstracting out more complex social group structures and social interdependencies, can also make it challenging for students to understand the concept of multilevel selection, which is required to explain the evolution or emergence of new levels of biological organization in the first place (e.g. Smith and Szathmáry 1995), as well as altruistic and cooperative traits in humans and other organisms (e.g. Wilson 2015). This aspect also has implications for emotional challenges stemming from an overemphasis on competition between (isolated) individuals (see below). A more generalized conception of evolution operating on various levels of biological organization also enables a transfer of the concept of population to the self, as a complex and changing system (e.g. highlighting complex systems dynamics such as feedback involved in phenomena such as homeostasis and behavioral regulation).

Fostering a stronger incorporation of the concept of system in evolution education by integrating interactions of many factors (environmental, social, organism traits, plus genes involved in…) beyond simplified gene-environment interactions, organism-environment interactions, or simplified genotype–phenotype relations, in evolving biological systems, may be achieved through the use of causal maps (e.g. Hanisch and Eirdosh 2020c), computer simulations (e.g. Centola et al. 2000; Goldstone and Wilensky 2008); and other teaching tools targeting systems thinking. This system's view on how evolution operates may also address other misconceptions such as teleological reasoning or genetic determinism (see above), as well as emotional and motivational hurdles.

Addressing challenges of evolution acceptance

The same elements of a trait-centered conception of evolution that might help make progress in evolution understanding as we described in the previous section, might also provide opportunities for making progress in the area of evolution acceptance (Fig. 2).

Table 3 summarizes some of the persistent challenges in evolution education related to evolution acceptance, as mediated by emotional and motivational factors as well as perceived relevance of evolution to student lives. We hypothesize that such challenges may be partly overcome in the following ways:

- Addressing challenges related to perceived relevance of evolution through greater emphasis on observable *cultural evolutionary dynamics* of human behavior, cognition and culture which are greatly impacting students' world and issues of sustainable development, as well as through *integrating student intuitive concepts* about change
- Addressing emotional hurdles due to emphasis on competition through greater emphasis on the *evolution of cooperative traits*, in humans and other species, the role of *social interdependence* impacting evolutionary trajectories across levels of organization, and exploring the example of *self as population* for how evolution can favor cooperation among interacting elements
- Addressing emotional hurdles due to emphasis on randomness and passiveness of organisms by greater emphasis on the *causal role of goal-directed behavior* in shaping evolution, and exploring the*evolution and development of our everyday experience*, including, sense of purpose, agency, belonging, intention, emotions, explicit goals, and values
- Addressing emotional hurdles due to deterministic and essentialist views of humans by greater emphasis on *complex developmental causes of human behavior cognition, and culture*, building on student intuitive concepts of adaptation, and relating to *self as an evolving system* or an *evolving population*
- Addressing challenges of evolution acceptance due to religious beliefs by focusing on *historic and current cultural evolutionary dynamics* that do not necessarily conflict with religious beliefs about the past, and by exploring the *evolution of religion and morality* and other valued behavioral and cultural traits.

Addressing challenges related to perceived relevance of evolution

Kinchin (2000, 182) noted regarding challenges to conceptual change, that "the context associated with the student's alternative framework may be perceived to have greater personal relevance than that associated with the scientifically accepted framework", which will hinder conceptual change. This highlights how conceptual understanding is tightly interlinked with emotional and motivational factors.

To foster a stronger integration of evolution concepts into students' everyday experience, Heddy and Sinatra (2013) and Pugh et al. (2010) employ a transformational approach developed by Pugh and Girod (2007), whereby educators model and make explicit how concepts covered in the classroom can relate to experiences outside the classroom, can expand one's perceptions of the world, and relate to one's values and personal interests. The authors find that these interventions increased conceptual understanding of evolution as well as positive emotions related to evolutionary theory compared to other interventions that target conceptual change but do not focus on these motivational aspects of meaning-making and transfer.

Many biology educators have also pointed out that teaching evolution through human examples or through examples that students experience in their everyday lives, may increase the perceived relevance of evolution understanding to students' lives and thus students' motivation to learn about evolution (Besterman and Baggot la Velle 2007; Nettle 2010; Pobiner 2016; Pobiner et al. 2018; Werth 2009).

However, examples for how evolutionary science affects or can be encountered in students' lives tend to focus on topics such as agricultural breeding, antibiotics resistance or evolutionary medicine–presumably because of the relevance of genetic variation in such examples, or broad ideas about how humans are related to the rest of life (e.g. Barnes et al. 2017; Heddy and Sinatra, 2013; Sinatra et al. 2008). Similarly, regarding the use of human examples, these tend to be constrained to those human traits that have a known and identifiable *genetic* basis, particularly morphological and physiological traits such as skin color, resistance to disease, lactose tolerance or

Table 3 Persistent challenges of evolution acceptance, possible sources of the challenges stemming from a gene-focused conception of evolution, and hypothesised opportunities for overcoming these challenges afforded by an interdisciplinary conceptualization of evolution

Persistent challenges to evolution acceptance	Possible sources of challenges stemming from a gene-focused conceptualization of evolution	Hypotheses for how teaching evolution from a generalized conception may help make progress
Relevance of evolution to student lives	The focus on genes greatly constrains the range of examples of evolutionary change relevant to student lives (traditional examples include e.g. evolutionary medicine, agricultural breeding, malaria resistance, skin color), including in the future A lack of integration of student intuitive concepts about observable change can reinforce the notion that evolutionary dynamics are not relevant in the explanation of phenomena of interest	Cultural evolution as well as gene-culture coevolution of behavior and cognition, opens up the space of possibilities for how evolutionary history and evolutionary change relates to students' everyday lives and to sustainable development in the present and future Integrating student intuitive concepts such as about mechanisms of variation and transmission of behavioral and cultural traits in the discussion of cultural evolutionary phenomena
Emotional hurdles due to emphasis on competition	Focus on competition and on individuals as primary levels on which selection occurs ("survival of the fittest"), at the expense of multilevel social evolution and the evolution of cooperation	Emphasis on the evolution of cooperation and prosociality in humans and other animals, as well as on major transitions in individuality throughout evolutionary history Emphasis on the evolutionary consequences of *social interdependence* and of selection as operating on multiple levels
Emotional hurdles due to emphasis on randomness and passiveness of organisms	Focus on "randomness" of genetically induced variation, and organisms being passively at the mercy of a "selecting environment" at the expense of goal-directed and niche construction activities of animal behavior De-emphasis on evolutionary explanations of behavior and cognition experienced by students as part of their identity (e.g. sense of purpose, agency, belonging, as well as emotions, explicit goals, values)	Emphasis on the causal role of behavior as selection pressure in evolution, and on the role of niche construction, especially in human evolution in the past, present and future Exploring the (complex) evolution and development of our everyday experience, including, sense of purpose, agency, belonging, as well as emotions, explicit goals, values
Emotional hurdles due to deterministic and essentialist views of humans	Focusing on changes in gene-frequency and simple genotype–phenotype relations creates a sense that one's traits are "set in stone" and downplays the role of experience, learning, social environment and other factors in development	Transferring the concept of population to the self, and integrating students' intuitive understanding of individual-level adaptation, can create a more flexible attitude towards self and others Teaching the complex evolutionary and developmental causes of human behavior and cognition, including cognitive biases towards essentialism and ethnocentrism
Challenges with acceptance of evolution due to conflicting cultural/religious beliefs	A focus on macroevolutionary deep time challenges religious beliefs on the origin of life, at the expense of teaching (micro-) evolutionary concepts by focusing on currently observable phenomena (esp. cultural evolutionary phenomena)	Teaching about concepts of variation, trait transmission and selection through cultural evolution examples that build on existing intuitive concepts and does not (initially or fundamentally) challenge religious beliefs Exploring the cultural evolution of religion as well as the cognitive foundations of religion and morality

adaptations to high altitudes (e.g. Andrews et al. 2011; Nettle 2010; Pobiner 2016).

In contrast, there seems to be a lack of educational materials and research concerning the (past, present, and future) evolution of human behavior, cognition and culture (Furrow and Hsu 2019; Legare et al. 2018; Ziadie and Andrews 2018). Yet, it is well known that in our species, genetic variation is rather small compared to the large amount of behavioral, cognitive and cultural variation. As Wilson (2005) laments, "One of the biggest tactical errors in teaching evolution is to avoid discussing humans or to restrict discussion to remote topics such as human origins." (Wilson 2005, 1003).

One example of an educational intervention that does explicitly apply evolution to human behavior is an interdisciplinary undergraduate course "Evolution for everyone" (O'Brien et al. 2009; Wilson 2005). Wilson (2005) documented change in students' answers to the question "How much has this class changed your views on evolution and its relevance to human behavior, on a scale from −10 (negative change) to +10 (positive change)?", where the majority of students indicated a large shift in the positive direction. Qualitative answers included phrases like "I have always agreed with evolution but I did not know how much of everyday life was affected by it." and "I came into the class not knowing a lot about evolution. I now have an entirely new outlook on how evolution can be applied to many aspects of life." (p. 1001).

Thus, exploring the evolutionary origins of human behavioral, cognitive and cultural phenotypic diversity in evolution education would greatly expand the available examples of trait variation in our species, with the potential to greatly enhance students' motivation to understand and apply evolutionary theory to many areas in their lives. Classroom discussion can then focus on the mechanisms that produce that variation, and that lead to the selective transmission or inheritance of traits, on a trait by trait basis (see Table 2, Additional file 1). In line with best practices for conceptual learning (see above, Stern et al. 2017), we hypothesize that repeated engagement in such an approach across general education may, in turn, advance conceptual understanding of evolution.

Similarly, a fruitful discussion in the classroom that may spark students' interest and motivation to learn about evolution, is about how humans might continue to evolve in the future. In educational discourse and textbooks (see Hanisch and Eirdosh 2020b), we find that such discussions tend to revolve around genetic changes alone. In contrast, looking at present and future human evolution from the perspective of cultural evolution (including gene-culture coevolution) may be a more relevant lense on how humans will continue to evolve. Arguably cultural evolutionary change will impact students' lives more dramatically and visibly compared to changes in gene frequencies. In this regard, the cultural evolution of *sustainability relevant traits* (see e.g. Brooks et al. 2018), such as cooperation, moral reasoning, or public health issues, can make evolution education also relevant to sustainability education (see also Eirdosh and Hanisch 2020).

For example, a classroom discussion in Andrews et al. (2011) revolved around 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. From the discussion (Andrews et al. 2011, supplemental materials), students are meant to learn that humans are *not* evolving to become fatter because the trait does not have a purely genetic basis, and humans who are more fat do not have more offspring. However, the concepts of *genetic* variation, *genetic* inheritance, and natural selection by differential reproduction would not be sufficient to explain the spread of such a complex phenotypic trait. Instead, from the perspective of a more generalized evolutionary theory, an exploration of the distribution and spread of a trait such as obesity would be more constructive for evolution education by considering a *variety* of possible mechanisms of inheritance (including social learning and ecological inheritance), as well as a *variety* of possible mechanisms of differential spread, as in fact already hinted at by the students themselves (see Hanisch and Eirdosh 2020b, for a discussion). In this way, this exploration may be more fruitfully related to issues of public health in human populations, which can help make students more appreciative of the role of evolutionary thinking for addressing real world problems.

Arguably, the lack of educational materials on the evolution and development of human behavior and cognition may stem partly from the scientific and moral questionability of reducing such behavior and cognition to genetics alone. This is achallenge that seems irreconcilable if phenotypes are conceived of as mostly being a direct result of genotypes (see Fig. 3). In contrast, a trait-centered conceptualization of evolution would allow the discussion of the evolution and development of such behavioral, cognitive and cultural traits because the causal factors that lead to such phenotypes explicitly include the social environment, social interactions, social learning and teaching, and other developmental factors. In fact, in the variation of many cultural phenotypes, genetic variation plays hardly any causal role at all (and is at best merely correlated due to common underlying causes such as historic migration patterns).

Addressing emotional hurdles due to emphasis on competition

Popular conceptions of evolution as "survival of the fittest" imbue a sense that the theory is all, and perhaps only, about competition among individuals. Across assessment tools and educational standards (see Hanisch and Eirdosh 2020b), we find that the role of competition in evolution, as well as individuals as primary levels on which selection occurs, are emphasised to such a degree, that it might make it challenging to conceive of how altruism and cooperation can evolve. In this regard, Centola et al. (2000, p.166) state that "many students who have been taught to think of individuals as discrete parts of an evolutionary system, have a difficult time understanding how cooperation, or altruistic behavior, could evolve. Because students' intuitions about evolutionary theory have been based on a model of individual success that does not consider the complexity of natural systems, many have had a difficult time re-framing their understanding of evolution." As highlighted above, Brem et al. (2003) found that students overwhelmingly considered that evolution justifies selfish behavior. Such notions, namely a lack of understanding about how evolution can favor cooperative, altruistic or prosocial behaviors in humans and other animals, may indeed affect the degree of evolution acceptance regardless of factors related to religious objections.

In contrast, trait-centered, generalized conceptualizations of evolution are concerned with how evolution operates across all levels of biological organization, and how social structure and social interdependence affect evolutionary dynamics (e.g. Aktipis 1016; Wilson 2015; see Hanisch and Eirdosh 2020a). Such concepts are necessary to understand the evolution of higher biological levels of organizations from lower levels in the first place (e.g. from populations of cells to multicellular organisms; termed major transitions, Smith and Szathmáry 1995), and to understand the evolution of cooperative and prosocial behavior, particularly in the evolutionary history of our own species (e.g. Bowles and Gintis 2011; Tomasello 2009).

Centola et al. (2000) document how undergraduate students from diverse disciplines were able to come to a new understanding about how altruistic behavior could evolve under specific environmental and social conditions by exploring a set of simple agent-based models, concluding that "students became increasingly sensitive to the difficulties of the 'problem' of altruism and were able to meaningfully speculate about the implications of these models for understanding the relevance of altruism and cooperation at a human scale." (p. 173).

Wilson (2005) describes a small classroom activity based on a number of scenarios that quickly allows students to understand how cooperative social behavior that we commonly term "moral" could have evolved and be adaptive, but also how it can be undermined by selfish behavior and therefore be maladaptive. Wilson (2005) states that "When evolutionary theory is presented as a framework for understanding these patterns in all their complexity, including the good, the bad, the beautiful, and the ugly, it is perceived as a tool for understanding that can be used for positive ends, rather than as a threat." (p. 1005).

This understanding of the evolution of cooperation can also be expanded to understand the evolution of multicellularity, thus applying multilevel selection to the individual as a highly integrated population of cooperating elements (e.g. Bonner 2000; Kirk 2005; Pfeiffer and Bonhoeffer 2003).

Addressing emotional hurdles due to emphasis on randomness and passiveness of organisms

If evolutionarily relevant variation is primarily conceived of stemming from randomly occurring mutations or genetic recombination, this might create emotional and motivational hurdles related to the role (or lack thereof) of one's own actions and choices, as it leaves little room for students to view themselves as active agents of change in how our societies, even our species, might evolve in the future. That is, students may adopt a view that 'my goals, choices, and behaviors ultimately do not matter in how humans will continue to evolve'. Additionally, a certain "existential anxiety" (Legare et al. 2018) may also be reinforced if organisms are largely being portrayed as passively at the mercy of a "selecting environment", rather than as actively involved in changing their environment, through the concepts of niche selection and niche construction. Such notions may underlie findings such as those by Brem et al. (2003), that even among students who "understand" evolution and who have no religious objections to evolution, there are a number of negative attitudes regarding how evolution inhibits self-determination and sense of purpose.

Conversely, trait-centered, generalized conceptualizations of evolution include an explicit causal role of behavior as shaping selection pressures, and emphasize the role of niche construction, that is, organisms actively changing their environmental conditions, which in turn has downstream consequences on evolutionary trajectories (Odling-Smee et al. 2003). This is especially relevant in human evolution (e.g. O´Brien and Laland 2012; Zeder 2016). Integrating and emphasising the role of our own behaviors and choices and of cultural evolutionary dynamics when reflecting on present and future human evolution may contribute to creating a more active stance and a higher motivation in students to understand how their choices and actions can shape evolutionary dynamics. That is, students may adopt a view that 'my goals, choices, and behaviors matter in how humans will continue to evolve'.

Additionally, a gene-focused conceptualization of evolution makes it difficult to explore the evolutionary and developmental origins of human behavioral and cognitive traits experienced by students as part of their identity (sense of purpose, sense of belonging, sense of intention and control, emotions, language, music, explicit goals, values), presumably because such traits can not be easily explained by genetic variation and inheritance alone. Conversely, trait-centered, generalized conceptualizations of evolution allow the exploration of the evolution and development of our everyday experience, as emerging from complex interactions between genes, socio-cultural environment, and interactions among phenotypic traits during development (see Fig. 3).

Addressing emotional hurdles due to deterministic and essentialist views of humans

Another set of challenges relates to social-emotional learning and students' attitudes towards themselves and others. We argue that focusing on changes in gene-frequency and simple genotype–phenotype relations may create a sense that one's traits are rather "set in stone" from birth and downplays the role of experience, learning, social environment, behavioral flexibility and other factors operating during development. This challenge is therefore also related to the cognitive biases of essentialist thinking and genetic determinism (see above), applied to the self, as well as the problem that students' intuitive understanding of individuals being able to adapt is considered a misconception (see above).

Instead, it may be valuable to drive students' reflection on their experience of being able to change, vary their behaviors, try out and learn new things, and of being able to (consciously) influence which kinds of behaviors they should "retain" into their (significantly unconscious) behavioral repertoire (see Table 2). Such an approach may be particularly critical as these processes underpin important educational constructs of social-emotional learning, such as growth mindset(Haimovitz and Dweck 2017) and psychological flexibility (Hayes et al. 2012; Kashdan and Rottenberg 2010). In this regard, transfering the concepts of *population* and *complex system* to the self can create a more flexible attitude towards self and others, as this mindset about the self is also considered a key process involved in mental health (Hayes et al. 2012; see Eirdosh and Hanisch 2020; Hanisch and Eirdosh 2020a).

Additionally, a more flexible attitude towards the self may also contribute to alleviating the problem of racist or ethnocentric thinking towards groups of other humans, a concern that is particularly relevant to how we teach about evolution (e.g. Kattmann 2010). This aspect highlights that teachers need guidance in how to prevent misinterpretations of evolution which embolden ethnocentric thinking.

In this regard, current approaches to tackle racism within the biology curriculum tend to focus on addressing the invalid notion of "race" from a biological perspective based on the low genetic variation in our species. We argue that this approach may not be very effective and perhaps even problematic, because it does not tackle the causes of ethnocentric thinking itself. Logically, it seems to invite the inference that, if genetic variation across groups of humans were indeed larger, racism would therefore be justified.

Instead, we argue that a generalized notion of evolution can help address racism in two ways. One way is through a focus on the traits that are common to all humans and on the complex developmental causality of human behavioral, cognitive and cultural phenotypes. In fact, cultural evolution models for the inheritance and spread of human behavioral, cognitive, cultural traits have precisely challenged the notion that certain traits (such as IQ, Cavalli-Sforza and Feldmann 1973) have a purely *genetic* basis–a notion which has been the basis of eugenic ideas about the superiority of certain ethnicities. Another way to address ethnocentrism within evolution education is to explore the evolutionary and developmental origins of human ethnocentric tendencies as well as ways to overcome them. This can be achieved in the classroom by exploring a range of developmental and cross-cultural research that highlights the human tendency to favor those who are similar to oneself in various, often superficial and arbitrary, traits (e.g. Hamlin et al. 2013). Furthermore, explaining the evolution of ethnocentric behavior can benefit from concepts in multilevel selection since it involves accounting for inclusive fitness, and can be explored in the classroom with the help of agent-based computer simulations (Hammond and Axelrod 2006; Wilensky 2003).

Exploring this content can help students become more aware of such tendencies and their causes, and subsequent discussions can focus on the implications for current society, and on various approaches and opportunities for overcoming such biases as individuals and as communities (see e.g., OpenMind Platform, Inc., 2020, for a successful evidence-based implementation of such an educational approach).

Addressing challenges with religious beliefs

Evolution education has a particular challenge regarding the acceptance of evolutionary theory due to perceived conflicts with individual beliefs about origins of life. As we highlighted above, while progress has been made in terms of increasing acceptance of evolution by teachers and the identification of effective approaches to help students and teachers reconcile evolutionary theory with their beliefs, there are still substantial challenges of acceptance, that in turn may hinder a conceptual understanding of evolutionary concepts.

We hypothesize that a generalized conception of evolution that includes cultural evolution, may allow the teaching about microevolutionary processes and concepts of variation, trait transmission and selection of historic and currently observable phenomena (esp. cultural evolutionary phenomena) without (initially or fundamentally) challenging religious beliefs about the past, and integrating student intuitive ideas about change. Even if acceptance of macroevolutionary facts about the past may be difficult to achieve, we may still be able to develop in students, regardless of their beliefs, understanding about concepts in evolutionary change, and this understanding may in turn enable a more open stance towards transferring concepts of cultural evolution to biological evolution.

Further, as discussed across multiple sections above, the potential to engage students in understanding the cultural evolution of sustainability relevant traits, morality and prosociality, and valued goal-directed behaviors may speak to the virtues and values of religious communities, and reduce concerns that evolutionary theorizing implies a justification of unethical behaviors (see e.g. Brem et al. 2003; Wilson 2005).

Is evolution education climbing the wrong mountain?

Evolution education continues to struggle with the range of persistent challenges to understanding and acceptance as outlined in this article. While some progress is being made as we highlighted above, we argue that the constraints provided by a gene-centered conceptualization of evolution may inherently limit the degree to which the evolution education community might make progress on these specific aims.

Remaining exclusively committed to the idealized, gene-focused ways of evolution conceptualization in standards, instructional methods, and assessment tools constrains pedagogical variation in such a way that it may well prove to keep the evolution education community stuck in a "local maximum" in the educational fitness landscape. While progress might be made on the way by tinkering with small variations of traditionally held conceptualizations, that same trajectory might end up removing the community more and more from reaching a more global peak, both for understanding and acceptance, that is potentially presented by an interdisciplinary evolution education (Fig. 4).

Enabling the evolution education community to reach its actual goals of wide-spread evolution understanding and acceptance in the classroom and in the wider public may thus require a leap into uncertain terrain. Relative to the familiar paths of existing methods and conceptualizations, this emerging landscape requires exploring new variations of educational approaches and new variations of research and assessment tools. But without such a leap, we are skeptical that the community will really be able to take advantage of the actual advances, in terms of conceptual clarity, nature of science lessons, applied value to students' everyday life, and to shaping the future

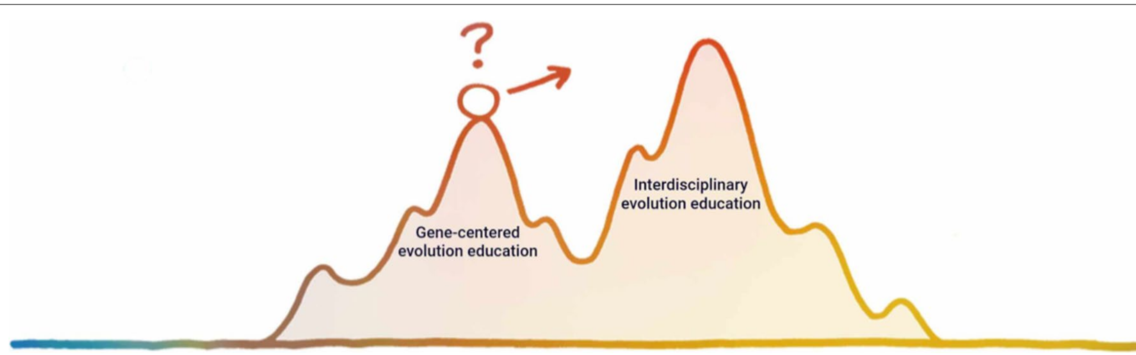

Fig. 4 The metaphor of a fitness landscape (commonly used in evolutionary biology and equally useful in cultural evolution science) to illustrate how progress in evolution education research might be inherently constrained to a lower-level potential that is defined by gene-focused conceptualizations of evolution, compared to the higher-level global potential that might present itself by embracing a more generalized, interdisciplinary conceptualization of evolution. Here, fitness peaks may correspond to varying degrees of cultural acceptance or depth of transferable conceptual understanding of core evolutionary theory. Figure adapted with permission from Jurgen Appelo: https://www.flickr.com/photos/jurgenappelo/with/5201851938/

evolution of our species, that evolutionary science itself is providing in the 21st century.

Outlook

We have outlined a number of hypotheses for how teaching evolution through a more generalized conception, informed by current discourse in interdisciplinary evolutionary science, may help overcome a range of persistent challenges in evolution education. This applies to evolution education more broadly, but especially to the treatment of human evolution, where many gains could be made, in terms of advancing an integrated and transferable conceptual understanding of how evolution operates across domains and levels, and in terms of advancing the perceived relevance of evolutionary theory to students' lives by incorporating the exploration of behavioral, cognitive, and cultural traits.

We recognize that empirical investigations of the validity of our hypotheses are a large endeavour, for which cooperation among many educators and researchers will be needed. Towards this aim, we have advanced a range of teaching and assessment tools as well as scientific content to engage teachers and students in generalized conceptualizations of evolution, with preliminary evidence of the learning potential in classrooms. Specifically, we have initiated and suggest the need for continued development of:

- The use of causal maps to highlight and reflect on the role of proximate mechanisms and complex causal interactions between natural environment, social environment, behavior, body features, brains, genes, and culture in development and evolution. Preliminary evidence from 10th and 12th grade classroom interventions indicates that causal maps can serve as an effective tool for reflection and discussion of complex causes of human behavior and cognition (Hanisch and Eirdosh 2020c);
- The use of analogy maps to discuss and practice the transfer of concepts in evolution between different conceptualizations or different domains (e.g. genes vs. culture vs. individual learning; see Table 2 and Additional file 1). With the help of such analogy maps, students' existing understanding about evolutionary concepts can be fruitfully expanded and deepened by transferring concepts from genetic evolution to other domains, or vice versa;
- The use of computer simulations to advance transferable understandings of concepts and processes in evolution (see e.g., Centola et al. 2000; Goldstone and Wilensky, 2008);
- Stronger integration of behavioral, cognitive, and cultural science perspectives, in addition to classic foci of genetics and archeology, in teaching about human evolution. Specifically, cross-species, cross-development and cross-cultural behavioral experiments and observations provide a wealth of largely untapped potential for the development of educational content (see Global ESD, 2020). Engaging such content may help identify a number of misconceptions about human behavior (see e.g. Hanisch and Eirdosh, in press), and at the same time may provide transformative experiences (sensu Pugh 2011) in the evolution education classroom, by allowing students to make connections to their everyday experience, extend their understanding, and explore implications for sustainable development.

While highlighting these potential pathways to overcoming persistent challenges in evolution education, we recognize that teaching evolution from a trait-centered, generalized, and interdisciplinary conceptualization may be met with skepticism and various objections. For example, the structure of school subjects and educational standards is currently such that it makes it difficult to explore the interdisciplinary nature of evolutionary theory in classrooms, particularly in relation to human sciences. In the US, the Next Generation Science Standards (Achieve 2013) explicitly exclude the human behavioral sciences from their framework (National Research Council 2012), while the social studies state standards (National Council for the Social Studies 2013) do not include the biological study of human behavior as part of the disciplinary core concepts.

Our claim is only that the evolution education research and development community should be actively engaged in this timely discussion around the educational value of an interdisciplinary evolutionary science, towards shaping the future curriculum. Overall, our project, *Teaching evolution as an interdisciplinary science*, aims to clarify the scientific landscape, learning potential, and challenges of moving in this direction. We feel there is a significant case for much broader engagement across the evolution education and other disciplinary education communities about the issues identified here. The role of interdisciplinary evolutionary theory in helping our species explore ways to adapt sustainably into the future is too important to not be taken seriously by educators. We encourage readers to join us in advancing this discussion.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s12052-020-00138-4.

Additional file 1: Comparison cultural evolution and genetic evolution. LessonPlan.

Abbreviation
MS: Modern synthesis.

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This article is part of a wider educational project by the authors on teaching evolution as an interdisciplinary science. See the project page on OSF: https://osf.io/u6rd5/.

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SH and DE developed the concept of the article. SH lead the writing of the manuscript. Both authors read and approved the final manuscript.

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ARTICLE

Causal Mapping as a Teaching Tool for Reflecting on Causation in Human Evolution

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Abstract
Teleological reasoning is viewed as a major hurdle to evolution education, and yet, eliciting, interpreting, and reflecting upon teleological language presents an arguably greater challenge to the evolution educator and researcher. This article argues that making explicit the role of behavior as a causal factor in the evolution of particular traits may prove productive in helping students to link their everyday experience of behavior to evolutionary changes in populations in ways congruent with scientific perspectives. We present a teaching tool, used widely in other parts of science and science education, yet perhaps underutilized in human evolution education—the causal map—as a novel direction for driving conceptual change in the classroom about the role of organism behavior and other factors in evolutionary change. We describe the scientific and conceptual basis for using such causal maps in human evolution education, as well as theoretical considerations for implementing the causal mapping tool in human evolution classrooms. Finally, we offer considerations for future research and educational design.

Abbreviations
DBIR Design-based implementation research
PCK Pedagogical content knowledge

1 Introduction

Humans have evolved an elaborate capacity to develop and act on our own intentions and those we perceive in others (the latter a component of *Theory of Mind*; Dunbar 2003; Whiten

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and Erdal 2012). These evolved capacities for the perception of needs, for goal-directed behavior in response to those needs, and for intentional reasoning are known to pose challenges in understanding evolutionary processes. Evolution educators and students alike may find it challenging to resolve the populational and stochastic aspects of evolutionary processes with the directed changes associated with our experience of needs and intentional action. Such challenges to evolution education are one facet of a broader class of *teleological reasoning*, the appeal to function, need, or purpose in evolutionary explanations.

Even in light of such challenges, many education researchers have highlighted the potential for human evolution examples to cultivate understanding of general evolutionary concepts, e.g., because the topic is engaging, it connects to students' lives, or because concepts like variation are more salient in our own species (Besterman and Baggot la Velle 2007; Nettle 2010; Pobiner 2016; Pobiner et al. 2018; Werth 2009). Furthermore, because it concerns our own species, an arguably richer diversity of empirical research exists about the causes of our human traits. Paleoanthropologists, paleoclimatologists, evolutionary anthropologists, archeologists, comparative psychologists, primatologists, and geneticists are among the scientists each contributing methods and lines of evidence about similarities, differences, and evolutionary changes in environment, behavior, cognition, morphology, brain, genes, social organization, and culture in humans and other primates. These diverse streams of inquiry may help us construct a more interdisciplinary account of the evolution of our species, compared to other examples in biology education.

In this paper, we aim to show that these interdisciplinary strengths of human evolution science may also offer opportunities to address a number of issues regarding teleological reasoning in evolution education. In the following sections, we review how the concept of teleological reasoning has been defined in different ways, and that there remains debate regarding how or if student answers to specific prompts should be considered as incorrectly teleological. We argue that a more explicit clarification and exploration of the causal role of behavioral variation in the evolution of certain traits may help students to link everyday conceptions about the role of behaviors and needs, to the mechanisms of evolutionary change. Furthermore, we argue that causal mapping can be a potential teaching tool to visualize these dynamics across a range of traits.

1.1 The Problem of Defining Teleological Reasoning

Teleological reasoning has been defined in many different ways by biologists and philosophers (Mayr 1974) as well as education researchers. In the evolution education literature specifically, we find variations in the framing of teleological explanations such as reference to purpose (Legare et al. 2013), reference to function (Kelemen 2012), reference to the consequences rather than an antecedent of an event (Coley and Tanner 2015), or viewing natural phenomena as purposeful (Barnes et al. 2017). In earlier recognition of the challenges posed by issues of teleological reasoning in biological causation, biologists coined the term *teleonomy* (Pittendrigh 1958) to frame apparent goal-directedness in living systems within naturalistic causal explanation. Teleonomy refers to the fact that organisms do have goal-directed behaviors, which, just as many other traits, are outcomes of natural selection (Okasha 2018). In this article, we leave aside the kind of creationist teleology that posits the actions of a purposeful creator, and focus only on the problem of what Evans and Rosengren (2018) term *teleological realism*—naturalistic explanations rooted in the needs of living organisms.

Within teleological realist conceptions, further distinctions have also been made, each thought to indicate different underlying reasoning styles, and each drawing attention to more specific educational challenges and opportunities. For example, Legare et al. (2013) distinguish between need and desire-based explanations; Kelemen (2012) identifies categories of "basic function-based," "basic need-based," and "elaborated need-based" explanations; and Evans and Rosengren (2018) mention a "restricted teleology" as a reasoning style that refers to needs but not psychological states. Our focus is on these varieties of need-based conceptions in relation to teaching for conceptual change in human evolution.

1.2 Students' Explanations May not Reflect Problematic Teleological Conceptions

Besides the complexity of how teleological reasoning is defined and differentiated, there is the related complex discussion regarding whether apparent teleological language from students can be interpreted as faulty biological reasoning.

Education researchers have pointed out that often, we do not really know what a student is thinking because students are not given more prompts and opportunities to elaborate on their thinking (Kelemen 2012; Kampourakis and Nehm 2014; Gouvea and Simon 2018). Categorizing short student explanations based on simple phrases that students might use such as "in order to", "so that", and "because it needs it" may be problematic because these tell us very little about the nuances of their thinking. Gouvea and Simon (2018) and Louca et al. (2004) argue that students' explanations or endorsement of explanations may be much more context-dependent and dynamic compared to a view that these represent relatively stable cognitive frameworks for evolutionary reasoning.

Importantly, in this regard, it has also been argued that teleological reasoning per se is not necessarily a problem (Varella 2018; Legare et al. 2018; Zohar and Ginossar 1998). Our evolved human tendency to see functions, goals, and purposes can be appropriate and helpful in exploring the causes and functions of *biological* phenomena and explaining them to others. Such reasoning may foster "new research questions and discoveries when asking for reasons, roles, goals, strategies, and values using 'why?' and 'what for?' questions" (Varella 2018). Similarly, Mayr (1974) stated that "[t] he teleological dilemma (...) consists in the fact that numerous and seemingly weighty objections against the use of teleological language have been raised by various critics, and yet biologists have insisted that they would lose a great deal, methodologically and heuristically, if they were prevented from using such language." (p. 136). According to Varella (2018), teleological reasoning becomes problematic, among others, when: it is misapplied to all aspects within a domain, such as when all phenomena in biology are explained by having a function (adaptationism, Gould and Lewontin 1979), or when attributing internal desires or needs to all actions of biological agents (fundamental attribution error), or when attributing intention to all human actions (intentionality bias); or when it is misapplied to a different domain, such as when human-specific mental states such as explicit beliefs are misapplied to other biological organisms (anthropomorphic reasoning), or when function and design are invoked to explain nonliving physical phenomena including those that are not artifacts (promiscuous teleology or function compunction, e.g., Kelemen 1999).

1.3 Teleological Reasoning in Different Types of Causal Explanation

Some of the difficulty with identifying student reasoning as unscientifically "teleological" may also have to do with the fact that biological phenomena such as organism traits (e.g., behaviors, morphology, physiology) can be explained by different types of causes, which are not mutually exclusive but complementary, addressing different aspects of a full causal account. Two common frameworks employed in biology to distinguish between types of causes are Tinbergen's four questions (Tinbergen 1963) and Mayr's distinction between proximate and ultimate causes (Mayr 1961). For example, in terms of Tinbergen's questions, an observable behavior can be explained by its more immediate mechanisms (environmental stimuli, senses, nervous system function, mental states, physiology, etc.), by referring to its developmental history, by referring to the function that the behavior had and currently has for the organism itself and/or for its ancestors in terms of survival and reproduction (thus whether it might have come about by natural selection), and by the phylogenetic history of the trait. Explanations of a phenomenon with causes immediately preceding or lying in the individual developmental past are often equated with Mayr's *proximate* explanations, while explanations involving function and phylogenetic history are often equated with Mayr's *ultimate* explanations (Dewsbury 1992; Hladký and Havlíček 2013; Laland et al. 2012).

Of particular interest to the evolution education community is the role of teleological reasoning in explaining the *ultimate* or *evolutionary causes* of observed organism traits. When eliciting student explanations of evolutionary causes, two different aspects seem to be of concern: on the one hand is the question of to what degree explanations include a role of *proximate mechanisms* such as behaviors in the evolution of a trait; on the other hand is the question of to what degree evolution itself is considered to have a goal or proceed toward a goal or direction.

We suspect that often it may not be made clear to students what kind of causal explanation is expected of them, which may lead to educators incorrectly identifying a reasoning style as "wrong" or "teleological" (Gouvea and Simon 2018; Louca et al. 2004), when it may be an adequate response based on student interpretations of less specific prompts. Lombrozo (2009) manipulated prompts by asking students questions such as "Why do flowers have trait X", and some students were also asked for a functional explanation such as "What purpose might X serve?", and found that the large majority of students' explanations referenced proximate mechanism or function based on the nature of the question. Thus, students may sometimes be giving proximate explanations (including cognitive processes and internal states, such as "it feels like doing X", "it wants to do X") or functions ("it needs to do X", "it has the trait so that it can do X"), when explanations of a mechanism of past natural selection are expected of them—the problem being that this reference to cognitive processes, need, or function does not in itself explain how a trait came about through natural selection. For example, Coley and Tanner (2015) considered students' reference to a function as teleological, because they considered only reference to past events as appropriate. However, function *is* often an important aspect of a biologically appropriate explanation for the existence of a trait (see Tinbergen's questions above) whereby it is *implied* that the trait's function is an *antecedent* cause for its existence.

As Okasha (2018) highlights, "natural selection generates a feedback process in which a trait's effect causally influences its subsequent fate, thus showing the apparently teleological explanation to be causal in disguise." Evans and Rosengren (2018) point out that "intentions and desires are not viable "biological" causes in the sense that they cannot explain the emergence of adaptive systems." However, in a proximate sense, psychological states of animals *can be* considered viable *biological* causes of *behaviors*, but these need to be *combined* with population-level mechanisms (natural selection, drift…) if the goal is to explain the phylogenetic emergence of (morphological, genetic, …) *adaptations*. Nehm et al. (2012) state that "Students often believe it is not possible to solve the problem [of how a trait evolved] without knowing how the trait functions, which likely indicates the absence of an abstract model of natural selection". However, without knowing about whether and what functions a trait might fulfill (including possible detrimental or neutral consequences), it is unclear how one can correctly reason about its evolution without, for example, committing other reasoning errors such as adaptationism. Kelemen (2012) categorized as "basic need-based" those explanations which "do not elaborate any actual mechanism of change. This is true even though a biological survival need (...) is invoked as an antecedent causal trigger. Absent any explicit reference to underlying mechanism, basic need-based explanations therefore carry the implication that an animal's biological need has an intrinsic power to bring a heritable trait into existence by having direct transformational effects on an animal's underlying (genetic) nature". However, it may not necessarily be the case that one can infer this simply from such a student explanation. Students might not think that organism preferences bring about adaptive changes in *morphological* traits, but adaptive changes in behaviors, which can be a valid biological account in line with current biological thinking (see the following section). Note also that in the above quote, the phrasing "biological (survival) need" is used in a way that, by itself, does not seem to be considered problematic.

In fact, it has been argued that explanations referencing "need" or "function" for the existence of a biological phenomenon may be a shorthand intuitive understanding that the consequences of the need or function in the past would have brought about the phenomenon in the population, even if no explicit causal mechanism is given (Gouvea and Simon 2018; Lombrozo and Vasilyeva 2017; Wright 1976). This is in line with the point made by Evans and Rosengren (2018) that need-based explanations (as opposed to desire-based explanations) may provide a bridge toward biological explanations of evolutionary change by natural selection.

Other educators, on the other hand, seem to engage in a practice whereby students' use of the term "need" is being actively discouraged or suppressed, such as through "booing" as soon as a student utters this word (Bravo and Cofré 2016). Thus, different views exist in the evolution education community regarding whether the use of the word "need" as such is problematic, or whether it is rather the lack of integration of biological needs of organisms, and their goal-directed behaviors and other proximate dynamics, with the mechanism of natural selection.

In this regard, it is also noteworthy that the concept of "need" is often referenced and defined in biology science communication and textbooks. For example, Aunger and Curtis (2008) define need as "A task related to an evolutionarily significant aspect of an animal's ecological niche which requires goal-directed behaviour to solve". Fuentes (2018), in his textbook on biological anthropology, relates the concept of need to "socioecological selection pressures" and states that "All animals are subject to five basic kinds of challenges: the *need* to obtain food, to move around their habitat, to protect themselves from predators, and to compete for resources both with members of their own species and with other species." (p. 130, emphasis added).

Furthermore, when young students answer questions such as "What are trees for?" with "So that birds can live in them," this might not imply that they really think trees were made for this purpose, but that from the perspective of a bird, this is what a tree can be used for. Ojalehto et al. (2013) refer to this as relational-deictic reasoning style and highlight that in such instances, students might be thinking about valid ecological relationships among organisms and their environment, rather than a belief that things in nature are designed for a purpose, outside of that ecological relationship.

In this article, we aim to highlight how these concerns for teleological reasoning might be addressed by helping students to link proximate and ultimate explanations toward a biologically appropriate causal account of organism traits in evolution in general and in human evolution in particular. In the next section, we review discourse and findings in evolutionary and developmental biology of the last decades about the role of behaviors as causal factors in evolutionary change. We then introduce the use of causal maps in the classroom as a tool to help students and teachers reflect carefully on the specific (proximate) interactions between environments, organism behaviors, and other traits, and how these interactions can lead to (ultimate) population-level changes over evolutionary time. We provide an example of the use of such causal maps in reflecting on the evolution of upright walking in human evolution and provide considerations for classroom implementation.

2 Clarifying the Evolutionary Consequences of Behaviors for Evolution Education—Perspectives from Evolutionary and Developmental Biology

Evolution is a process by which small changes and interactions in the proximate timescale can have large population-level consequences in the phylogenetic timescale. How behavioral variation plays into these processes is a subject of much discussion in evolutionary biology. In this section, we argue that a renewed recognition within evolutionary biology of behaviors as significant drivers of (rather than merely outcomes of) evolution may provide opportunities for evolution education, namely by building on students' existing intuitive conceptions regarding the role of need, including individual behavioral responses to need, as causal factors in evolutionary change.

A comprehensive review of the sociology and history of evolutionary theory is beyond the scope of this paper (see, e.g., Corning 2014; Hanisch and Eirdosh 2020; Pigliucci 2009). Here, we focus only on the changing conceptualizations of the role of behaviors in evolutionary and developmental biology in relation to our discussion on teleological reasoning in evolution education.

In Darwin's time, nothing concrete was known about the specific mechanisms of variation that created the diversity of phenotypes within and across populations, nor about the specific mechanisms of inheritance that made offspring resemble their parents. Evolutionary theory in the second half of the twentieth century has been greatly influenced by the *modern synthesis* which incorporated insights from molecular biology and genetics into the concept of evolution by natural selection. After all, the discovery of DNA and the mechanism of its inheritance through biological reproduction seemed to make concrete how Darwin's theory of natural selection works.

In the 1950s and 1960s, biologists also discussed the possible roles of behavior and learning in evolution, such as behaviors possibly playing significant causal roles in adaptive radiations or as isolating factors in speciation, and that new behaviors may appear before genetic changes in driving evolutionary change (Roe and Simpson 1958; referenced by Corning 2014). Interestingly, in 1970, Mayr also wrote that "Behavior is perhaps the strongest selection pressure operating in the animal kingdom." (Mayr 1970, p. 388).

Indeed, many concepts in standard evolutionary theory do already incorporate the role of preferences and behaviors in evolutionary change. For example, in sexual selection and social selection, the preferences of others in the social group or population affect the fitness of an organism and, thus, the evolutionary change of gene frequencies in a population. In gene–

culture coevolution, cultural practices (behaviors, norms, technologies, etc.) can act as selection pressure on genes (Chudek and Henrich 2011; Laland et al. 2010). Clearly, in the evolution of some traits, behaviors and preferences (whether consciously held or not) are considered to play an explicit role as causal factors influencing selection pressures.

In recent decades, discussion on the role of behavioral variation, learning, and other factors operating during the *development* of organisms and potentially influencing evolutionary change has been rekindled. This is because biologists of various subdisciplines became aware of an increasing number of potential examples of such cases, and evolution science became more and more an integral part of those subdisciplines. Proponents of developmental systems biology highlighted that genes by themselves do not lead to phenotypes, but rather genes are one among many causal factors or resources, embedded in contexts rich in other resources that are also often causal factors in the development, or *reconstruction*, of particular phenotypes (Griffiths and Gray 1994; Oyama et al. 2001). This basic yet important insight is also being recognized among genetics education researchers (Jamieson and Radick 2017). In humans in particular, many observable phenotypes cannot be explained solely by random genetic variation, such as language, toolmaking, literacy, personality, or occurrence of particular diseases. As will be shown below, even causal explanations of the evolution and development of a seemingly "straightforward" phenotype such as upright walking may need to integrate developmental factors beyond genes.

Biologists also highlighted that the proximate–ultimate distinction may obscure the fact that proximate mechanisms are not always simply *outcomes* of evolution, but can also function as ultimate *causes* of evolutionary change:

> Standard evolutionary theory can recognise that plastic phenotypes are capable of fine-tuning their adaptations during their development, and may, thereby, affect their fitness. But it struggles to recognize that phenotypic plasticity can ever drive, or co-cause, evolution, through generating innovation, biasing variation, or imposing directionality on evolutionary trajectories. This externalism is a core assumption that causes problems for evolutionary biology and hinders integration of evolution with adjacent disciplines. (Laland et al. 2012).

Similarly, Corning (2014) states that "in practice, proximate and ultimate forms of causation interpenetrate; proximate causes associated with [behavioral choices] may also be responsible for shaping ultimate causes." Developmental biologists likewise began to point out that phenotypic plasticity may reposition the role of genes as sometimes being "followers" rather than drivers of evolutionary change (West-Eberhard 1998), a point that had already been made by Mayr in 1958 (cited by Corning 2014).

Among the concepts that indicate a role of (goal-directed) organism behavior or preferences in driving evolutionary change are *niche selection* and *niche construction* (Odling-Smee et al. 2003; Laland and Sterelny 2006). According to these concepts, the preferences and behaviors of organisms can change the environmental conditions that the organism (and its descendants) finds itself in, hence changing selection pressures on organisms (and by extension, on genes). While in the 1950s, evolutionary biologists such as Dobzhansky asserted that "Man alone adapts himself, in a large part, by actively or even deliberately changing the environment, and by inventing and creating new environments" (Dobzhansky 1955, p. 339), biologists since then observed that in fact, many species actively alter their environments (with no "conscious intention" required), with more or less pronounced influence on evolutionary trajectories. Often cited examples are animals building nests and burrows or burying eggs, beavers building dams, ants cultivating fungi in gardens, animals preferring to forage for particular food sources in their environment, and earthworms loosening the soil thus influencing their environment and the environment that their offspring find themselves in. The behavioral choices organisms make, such as habitat choices and dietary choices, may be important initiators of adaptation of organisms to novel environments/niches, including currently observable adaptations to climate change or habitat destruction (e.g., Ducatez et al. 2020; Tombre et al. 2019), as well as responsible for major macroevolutionary adaptive radiation and speciation (e.g., Badyaev 2009; Dukas 2013; Moczek et al. 2011; Odling-Smee et al. 2003; Pfennig et al. 2010; Scoville and Pfrender 2010; Snell-Rood 2013). Humans are often considered the prime niche constructors, as our cultural behaviors have become the dominant force shaping our social and natural environments, which in turn provided selection pressure on human traits (Kendal et al. 2011; O'Brien and Laland 2012; Zeder 2016). The role in evolution of such behavioral variation emerging during development, and its inheritance through mechanisms of social learning, has been acknowledged in evolution education literature (e.g., Kampourakis and Zogza 2007), but it appears that these dynamics have not yet been explored in terms of how they may provide a bridge between student understanding of proximate causation and evolutionary explanations.

In concluding this review section, we argue that these developments in evolutionary and developmental biology point to opportunities to tackle a number of misconceptions in evolution education, including the question of how to deal with variations of seemingly teleological reasoning in students, particularly the reference to "need" and other proximate factors.

As the continued debate in evolution education shows, it may be profitable to take on these perspectives because they may allow educators to explicitly link students' everyday experience of proximate needs, goal-directed behaviors, and preferences to scientific conceptions of evolutionary change. When educators focus mainly on genes and gene–environment interactions when treating the evolution of traits, it may lead to the abstracting out of "all the biology in-between" (Laland et al. 2012), that is the interactions between environments, behavior and cognition, bodies, brains, and genes at multiple levels of organization and different timescales. This may be a shortcut that precisely creates intentional or teleological reasoning and other common learning difficulties in evolution education or that creates difficulty in distinguishing between appropriate vs. inappropriate reasoning styles of students. It is largely this "biology in-between" that students and all humans know from their everyday experience, whereas genes and wider population-level dynamics remain more abstract. Students, as biological organisms, simply experience various needs and their own behavioral responses to such needs ("I need to drink some water," "I need to go to the bathroom"), in their everyday lives. Furthermore, this "biology in-between" is what students also learn about in other topics within the biology curriculum—ecological relationships, niches, optimum conditions, structure and function, animal behavior, nervous systems, physiology, homeostasis, learning, etc. Is it possible that students bring that understanding to the table when asked to talk about the causes of traits, but they simply have not been given explicit tools to link their understanding of organism behavior, physiology, and ecology to evolutionary change? Additionally, asserting that, across the board, behaviors and preferences of organisms do not have a role in evolutionary explanations of traits leads to confusion when treating standard concepts in evolutionary theory such as sexual and social selection, a point also raised by Varella (2018).

To our knowledge, these perspectives on the role of proximate mechanisms in evolutionary change and resulting teaching opportunities currently appear to be not part of the discussion in the evolution education literature. In this regard, it is worth noting that in a review by Ziadie and Andrews (2018) on pedagogical content knowledge (PCK) about teaching concepts and topics in evolution, the authors identified no peer-reviewed studies that explored PCK elements for secondary education around the topic of evolution of behavior. Hence, there also appear to be currently no tools to support educators and students in being explicit and specific about the causal roles of behaviors and preferences, as well as genetic mutations and the mechanism of natural selection, in the evolution of particular traits.

Thus, specific teaching tools may help in closing this gap. Such tools may address, among others, the points raised by Gouvea and Simon (2018), Louca et al. (2004), and Ojalehto et al. (2013), namely that students may be explaining biological phenomena by referring to valid ecological relationships and functions that are then wrongly interpreted as teleological reasoning. In the next section, we propose the use of causal mapping as a specific teaching tool.

3 Causal Mapping for Teaching Behavior as Selection Pressure

In this section, we argue that causal mapping can be a potential classroom tool to help students and teachers to construct and reflect on causal frameworks that link organism behaviors, bodies, genes, and environment in a way that is congruent with biological thinking and allows student thinking to be made visible to themselves and teachers. Lombrozo (2009) and Lombrozo and Gwynne (2014) used a narrative form of such causal chains that link a proximate mechanism for a trait and the ecological function of that trait. Here, we show how causal maps can be used to visualize such linkages between proximate mechanisms, functions, and natural selection.

Causal maps, also called causal diagrams, are a subset of concept maps which focus on cause–effect relationships (links) between specific nodes, i.e. phenomena to be explained (e.g., Cox et al. 2018). Causal maps are a tool of reflection, inquiry, synthesis, and discussion in evolutionary science to disentangle and grasp the complex nature of causal relationships during the evolution of biological phenomena, particularly in evolutionary anthropology (e.g., Antón and Josh Snodgrass 2012; Chudek and Henrich 2011; Coward and Grove 2011; Koops et al. 2014; Laland et al. 2011; Whiten and Erdal 2012). Causal maps are also used in biology education, e.g., to visualize interactions between species in an ecosystem. Jamieson and Radick (2017) used causal mapping in a genetics course to highlight the complex relationships between multiple causal factors (including genes, developmental factors, behaviors) influencing each other and a focal phenotype such as cardiovascular disease. However, an informal content analysis of the human evolution section in 15 German high school biology textbooks (spanning grades, states, and publishers) revealed that only three textbooks used causal maps to depict a more complex nature of causality in human evolution (unpublished data). Among these causal maps, the nature of the causal arrows used is not further elaborated to teachers or students, posing the problem that this might invite teleological conceptions about change (e.g., Baack et al. 2016, p. 482, 493). Also, the section on primate (including human) evolution in a popular US biology textbook (Miller and Levine 2010) contained no causal explanations at all.

In causal maps, traits, conditions, species, or other factors form the nodes that are linked by arrows that mark some kind of causal relationship (X leads to, changes, or influences Y; Fig. 1a). Causal relationships can be of different nature. The concrete nature of a causal relationship can be specified if it is known or presumed, or not if it is subject to debate and reflection. For example, "is consumed by" is a commonly used causal link in causal maps of food networks (and the specific mode of consumption is a still more fine-grained mechanism). Alternatively, links categorized as merely “influences” can drive classroom discussions about the potential specific mechanisms.

“Natural selection” is a kind of causal relationship in which a condition “selects for” a trait, meaning that it favors an increase in trait frequency *in the population* and *on a phylogenetic timescale* due to differential survival and reproduction under those specific conditions (Fig. 1b). Environmental factors or other organism traits that enable, facilitate, or favor the *development* or expression of a particular trait mark another kind of causal relationship operating on the *level of the individual* and on a *developmental timescale*. Organisms have many different phenotypic and genotypic traits (behavior, morphology, physiology, cognition, genes, life history, social organization, etc.). These interact and influence each other in development and evolution, leading to trade-offs in the optimization of traits, or causally interdependent “trait packages” that are more or less functionally integrated and selected together.

In this regard, it is important to emphasize that not all traits are caused in the same way (Fig. 2). Sometimes a chance genetic mutation, creating a particular phenotype that provides survival advantages in a particular environment regardless of behavior, can be sufficient to explain the development, function, and resulting natural selection of a phenotypic trait (Fig. 2a). Sometimes, however, organism behavior (or other proximate, developmental factors) also has a causal role, particularly when considering morphological characteristics that provide a function in relation to certain behaviors such as feeding, mating, or locomotion. In such cases, morphological features such as beak size, neck length, or shape of the spine often do not have any consequences for natural selection in isolation, but their functions are tightly connected to an organism’s behavior (Fig. 2b). Particularly in human evolution, topics and concepts such as upright walking, meat-based diet, toolmaking, language, (self-)domestication, and gene–culture coevolution cannot be explained by referring to chance genetic mutations *alone*, and this might invite confusion or incoherence when the topic of human evolution needs to be treated under a generalized framework of evolution.

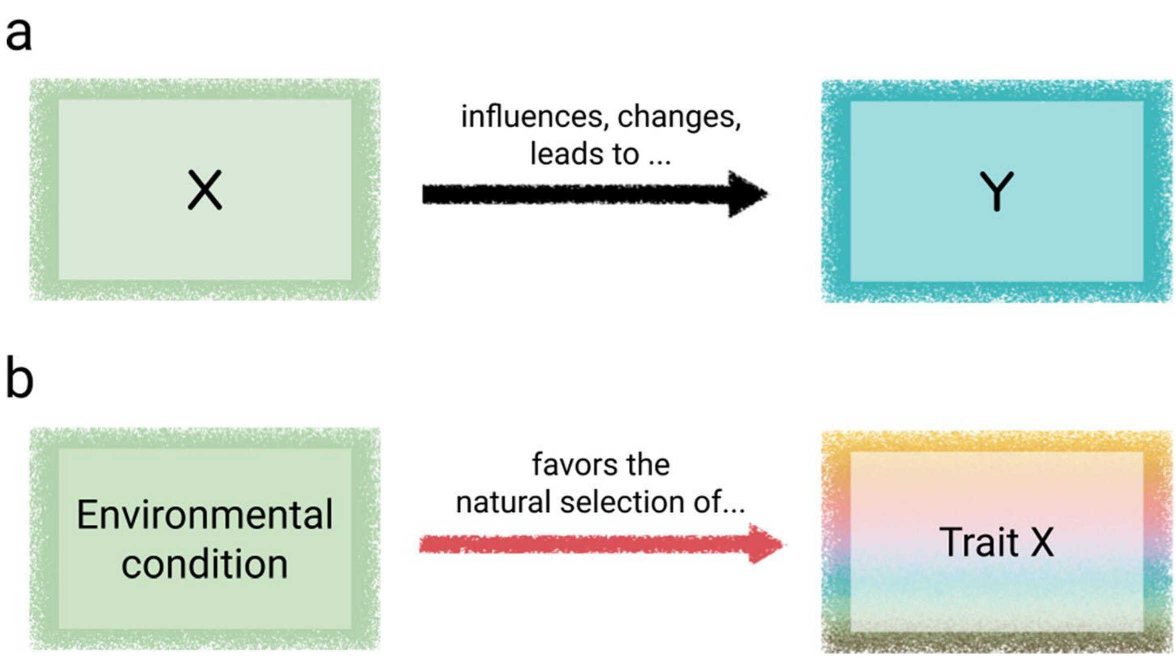

Fig. 1 Key elements of causal maps—nodes and arrows (**a**). An example of a specific causal relationship operating in the natural selection of traits (**b**)

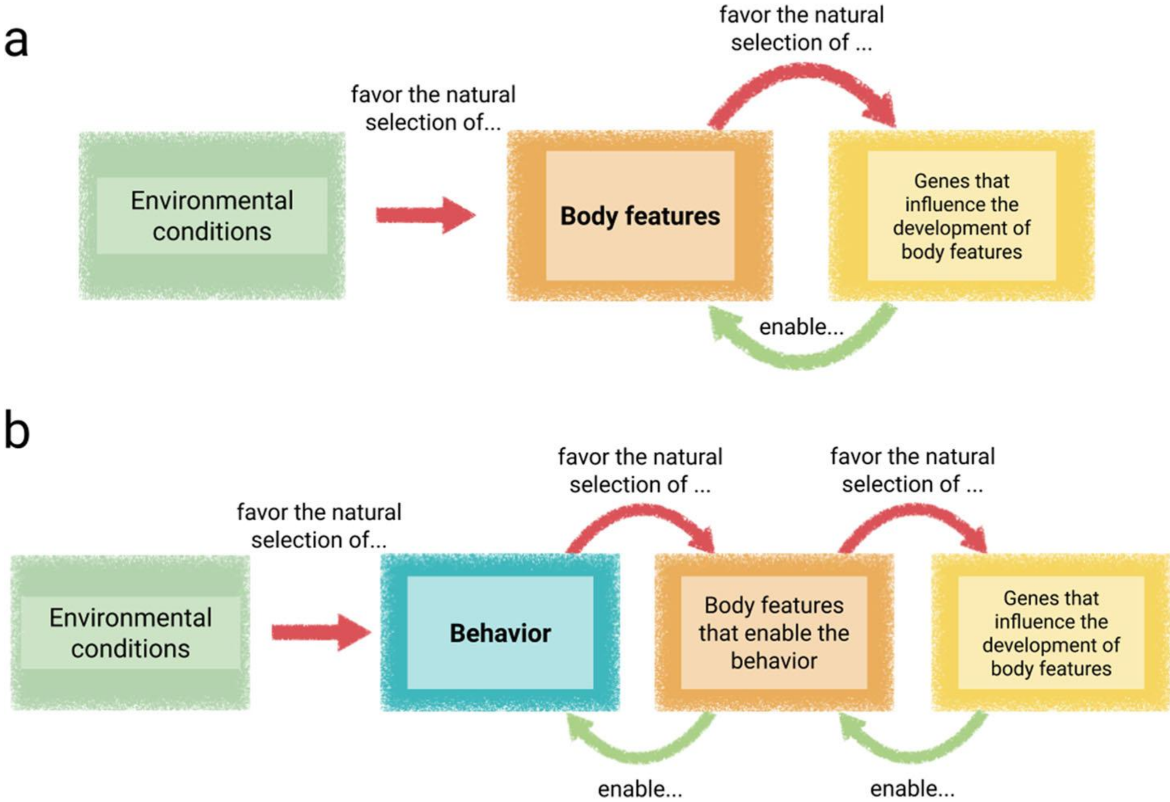

Fig. 2 Hypothetical examples of causal maps in which behavior may not have an important mediating role (**a**) and in which behavior has an important mediating role (**b**) in the evolution and development of a trait complex

Furthermore, causal maps may help put the role of genes in a larger developmental context, in line with perspectives from developmental systems biology (Oyama et al. 2001). For example, Jamieson and Radick (2017) designed an alternative genetics course that emphasized developmental processes rather than transmission and that emphasized phrases such as "gene(s) involved in" rather than "gene(s) for," using causal maps as a visualization tool. Results indicate that these modifications have the potential to alleviate notions of genetic determinism or essentialism, another set of well-known student misconceptions in biology education.

Of importance for the purpose of this paper is the fact that the directed causal relationship "needs, requires / favors natural selection of" explicitly links "need" or "function" to a causal mechanism of population-level change: if an organism *needs* or requires a particular trait, because it functions to enhance survival and reproduction (or in other words, to fulfill a survival and/or reproduction *need*) relative to alternatives under the given condition (the starting point of the arrow), we can say that there is "selection pressure" on those trait variants that are able to fulfill those needs better than other trait variants; thus, those trait variants are likely to become more common in the population through the mechanism of natural selection. These conceptions on the role of need are in line with how some biologists explicitly consider the concept of need in relation to selection pressures within an organism's niche (e.g., Aunger and Curtis 2008; Fuentes 2018; cited above).

In the process of constructing or reflecting on such causal maps, the specific causal mechanism of natural selection, which is a kind of sorting mechanism that operates on the level of the population, can (and should) be elaborated with the help of other teaching tools that target *population thinking* in order to convey the role of the other important core concepts of evolution by natural selection, namely variation, differential survival and reproduction due to trait variation, and inheritance (Andrews et al. 2011; Nehm et al. 2010; Petrosino et al. 2015). These concepts are likely foundational prerequisites to productive engagement with causal maps of human evolution. To this aim, we developed a "natural selection worksheet" that allows students to calculate and graph the change in trait frequencies in a population due to variation, differential reproduction, and inheritance (see classroom implementation considerations below and Online Resources 1 and 2). The resulting graph of the changes of trait frequencies in a population over time can serve as an icon to depict the population-level mechanism of natural selection (Fig. 3).

It is beyond the scope of this paper to address the wider discussion in biology about the generalized nature of "variation" and "inheritance," beyond genetic variation and inheritance (see, e.g., Jablonka and Lamb 2005; Laland et al. 2015; Mesoudi 2011; Odling-Smee and Laland 2011; Hanisch and Eirdosh 2020 for a conceptual clarification for evolution education). However, as the discussion in the previous section indicated, behavioral variation is increasingly considered by biologists to be a causal factor in evolutionary change. Causal maps that relate behaviors, body features, and genes can help students reflect on this issue, namely by drawing attention to the fact that without (more or less random) variation in the population and without an inheritance mechanism for that variation, a factor cannot ultimately contribute to population-level changes due to natural selection (see example section on upright walking below).

Thus, it would not necessarily be an instance of unscientific "teleological" reasoning to say that a trait exists because an organism (and its ancestors) has needed it or because it fulfills an

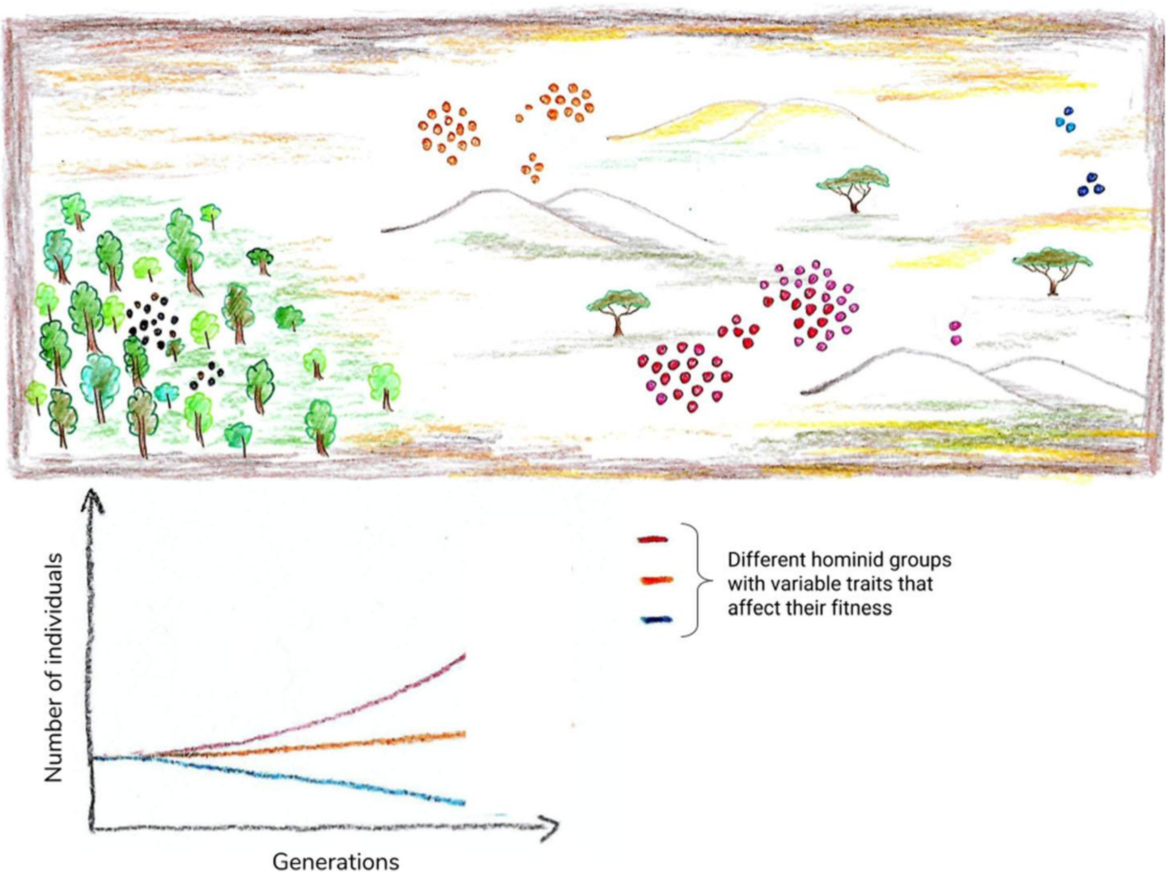

Fig. 3 Schematic drawings and population change graphs which can be reconstructed on classroom chalkboards while engaging students in discussion about *variation* in *populations* and *selection* processes acting on this variation

important function for the organism (with past natural selection implied as the causal mechanism for the existence of that trait); rather, this would reflect teleonomic reasoning (Corning 2014). Conversely, if a factor affects the natural selection or development of a trait in an organism, there is not necessarily strong selection on that factor because of this causal role, and hence, in that case, the factor cannot be said to exist because of its function for that organism—it simply exists and happens to affect the organism and/or the population in some way, or has a helpful function for the organism. The latter case relates to the relational-deictic reasoning style that, according to Ojalehto et al. (2013), may be an instance of correct reasoning about ecological relationships. Causal maps can help students and teachers see and represent the differences between such causal relationships. This distinction also helps to visualize important concepts in biology. For example, biologists distinguish between "cue" and "signal" based on whether a factor has undergone selection *because of its information function* to an organism (then it is called signal), or not (then it is called cue; Hasson 2000; Maynard Smith and Harper 2003; Fig. 4), and coevolution is a term to describe such instances in which natural selection between two or more species or factors "goes both ways." In this regard, Thompson (2010) argued for the importance of integrating concepts in coevolution into evolution education and used causal maps to depict selection arising from the interactions between species. Another concept in current evolutionary theory that such causal maps can help make more concrete is the notion of selection operating at multiple levels of biological organization, including genes, individual organisms, and groups of organisms (the latter being particularly important in exploring the evolution of cooperation; e.g., Okasha 2006; Sober and Wilson 1998; Wilson 2015).

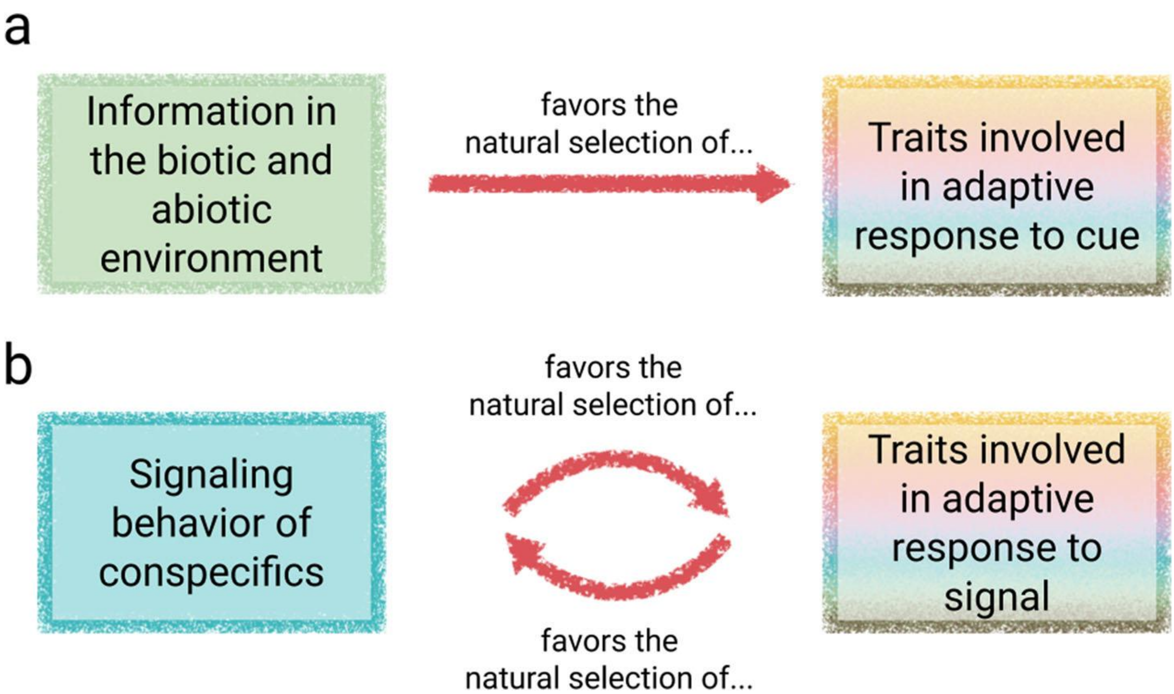

Fig. 4 Example of how causal maps can help differentiate between the instances in which natural selection is a causal mechanism for the existence of a factor or trait, and instances in which it is not, using the example of the difference between "cue" and "signal". **a** An abiotic (such as seasonal changes in day length) or biotic environmental factor (such as the rustling sound made by a prey animal) provides selection pressure for an adaptive response. The environmental factor has not been selected for that function to the organism, it simply exists. However, from the perspective of the organism, it has the function of eliciting a response—it is a cue. **b** A signaling behavior of a conspecific (such as an alarm call) provides selection pressure on other conspecifics for an adaptive response. The adaptive response requires the signaling behavior of conspecifics, which can come under selection *because of that function*

Furthermore, causal relationships between several factors can interact and lead to positive or negative feedback, thus reinforcing (positive feedback) or buffering (negative feedback) the degree of change in individuals, populations, and ecosystems, leading to the decentralized emergence of phenotypes, adaptations, or ecosystem-level properties. Particularly during human evolution, positive feedbacks between several traits and between traits and the (constructed social, natural, cultural) environment have led to the accelerating rate of change in human brain structure, behavior, cognition, and culture, often also affecting genes. Causal maps can visualize this complex nature of evolving systems and may help foster a more decentralized mindset or emergent property schema about the nature of evolutionary change (Cooper 2017; Petrosino et al. 2015; Xu and Chi 2016).

Because of these educational potentials, we have developed a teaching toolkit for causal mapping, specifically for the context of human evolution (Figs. 1, 2, 3, and 5), which allows educators to integrate these perspectives from evolutionary developmental biology and systems thinking. The causal mapping tool was developed through theoretical synthesis and iterative engagement by the authors within the context of a teacher–researcher collaboration in several German biology classes on the topic of human evolution. The tool can facilitate reflection on the specific causal relationships between the (sociocultural and biophysical) environment, behaviors, bodies, brains, and genes (Fig. 5) and how interactions between these may lead to changes in trait frequencies on the population level over time. In the following section, we show how causal maps may help in reflecting on the evolution of human traits, with a scaffolded example of the evolution of upright walking. Further below, we present considerations for the implementation of the causal mapping tool in the classroom.

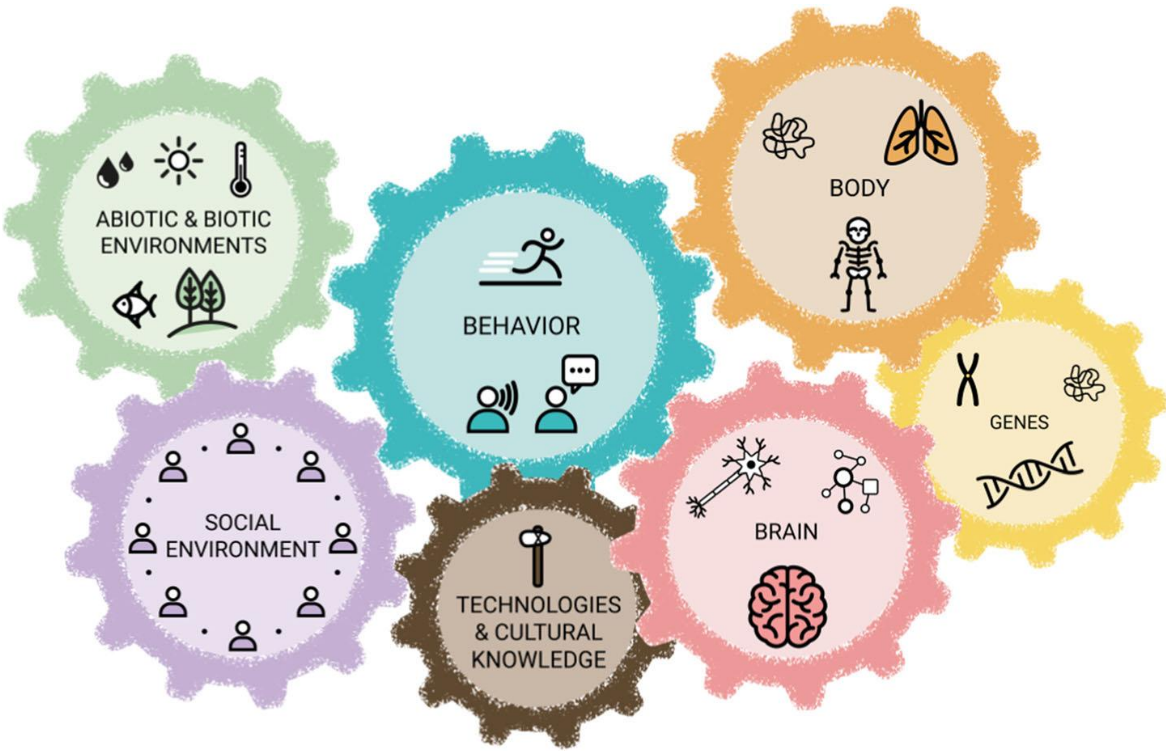

Fig. 5 *Causal domains* of abiotic and biotic environment, social environment, technologies and cultural knowledge (especially in the case of human evolution), behaviors (including cognition), body features, brains, and genes help sort the different causes possibly involved in the evolution and development of traits (while being clear that there are not necessarily strict boundaries between them). How do they interact to shape the evolution and development of traits and environments?

3.1 Example: Evolution of Upright Walking

The evolution of upright walking is, quite literally, an icon of evolution itself (Werth 2012; Fig. 6), a key element of popular narratives about the origins of our species. In this way, the evolution of upright walking is deeply linked on a conceptual level with the evolution of our human cognitive and cultural capacities (indeed it is the act of upright walking that, in some ways, freed our hands for gestural communication and tool use). It may well seem to students that human intentions and purposes for upright locomotion drove the evolution of this trait in our species. For these reasons, evolution educators and students may benefit by reflecting on the causes and consequences of the linked behavioral–morphological traits that enable our now obligatory upright posture. While upright walking is already a classical theme in human evolution classrooms, and many resources and publications already exist for educators (e.g., Kingdon 2003; Smithsonian Institution 2019), this section aims to highlight how the use of causal maps may serve as an additional tool to help integrate these existing perspectives and resources with further considerations from evolutionary anthropology. An example of a lesson plan on upright walking that integrates the perspectives from this section is given in Online Resource 4.

How did our species evolve the behavioral trait of habitual upright walking? We of course have to view this question in connection with the evolution of morphological features (e.g., position of the foramen magnum, shape of the spine and pelvis, and the length of the arms, legs, and toes) that favor this behavior, as well as genes that favor the development of these body features. What role might behaviors and preferences as well as genetic mutations have played in the evolution of these traits?

An important research paradigm for anthropologists trying to understand the nature of causal relationships during human evolution is the comparative method - comparing the traits and causal factors at play in the observable behaviors of primate relatives with those that might have been at play in the evolution of our hominid line (using archeological and paleontological

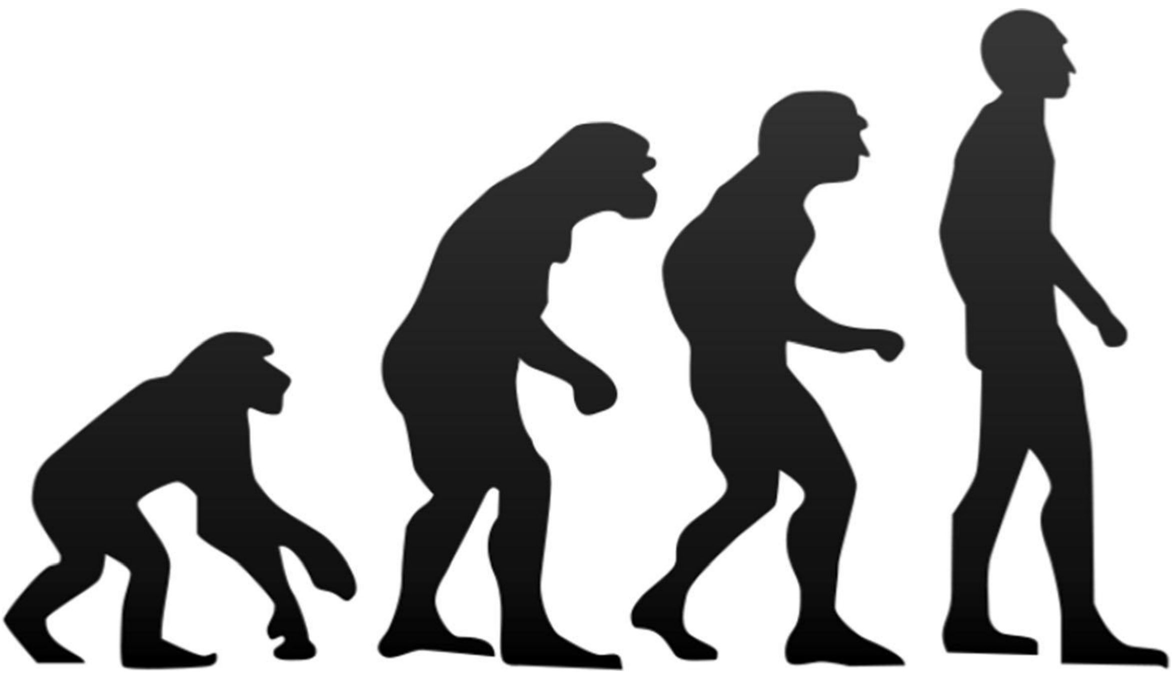

Fig. 6 "March of progress," an icon of evolution often associated with teleological, intentional, or progression-based conceptions of human evolution. Image source: Tkgd2007 (2008); CC-BY-SA 3.0) https://creativecommons.org/licenses/by-sa/3.0/deed.en. https://commons.wikimedia.org/wiki/File:Human_evolution.svg

data). This allows us to directly observe some important proximate mechanisms between the environment, behavior, and cognition of primates, and link them to possible outcomes over evolutionary timescales.

Anthropologists have been observing chimpanzee locomotive behavior under different habitat conditions in Guinea, which are marked by shrinking forested areas, a mosaic of vegetation and agricultural land (Carvalho et al. 2012). They observed that chimpanzees engaged in bipedal walking four times more often in habitats where there was low density of preferred food items, compared to habitats where valued food items were abundant or where food items were less valued. Furthermore, chimpanzees carried more than twice as many items (food as well as tools) when walking bipedally, using hands, mouth, and feet, compared to other modes of locomotion (Fig. 7). To anthropologists, these observations of chimpanzee behavior under environmental conditions that may resemble those faced by our ancestors serve as an indication or model to think about the natural selection of upright walking in our ancestors. Clearly, one can say that chimpanzee preferences (for certain food items, for gathering as many of them as possible, and for consuming them in a safe place with low competition from conspecifics) and chimpanzee behavior (bipedal walking *in order to*—because it allows to—carry as many valued food items as possible) play a role in the expression of the phenotype of upright walking behavior. However, the chimpanzee does not engage in the behavior of upright walking *in order to evolve* a different body structure, his goal is merely on the proximate level (get tasty food, consume it in a safe place). Furthermore, this (goal-driven) behavior alone does not necessarily lead to population-level *natural selection* of body features that enhance the expression of this behavior. It depends on the degree to which this behavior has consequences for survival and reproduction under the given environmental conditions.

Thus, observing chimpanzees that walk upright under certain conditions, and often with a clear goal (e.g., carrying food items to a safe place; Fig. 7), can be a narrative teaching tool for teachers and students to think more explicitly about the causal chain that, under specific conditions, *may* eventually lead to a change in the frequency of body features and genes

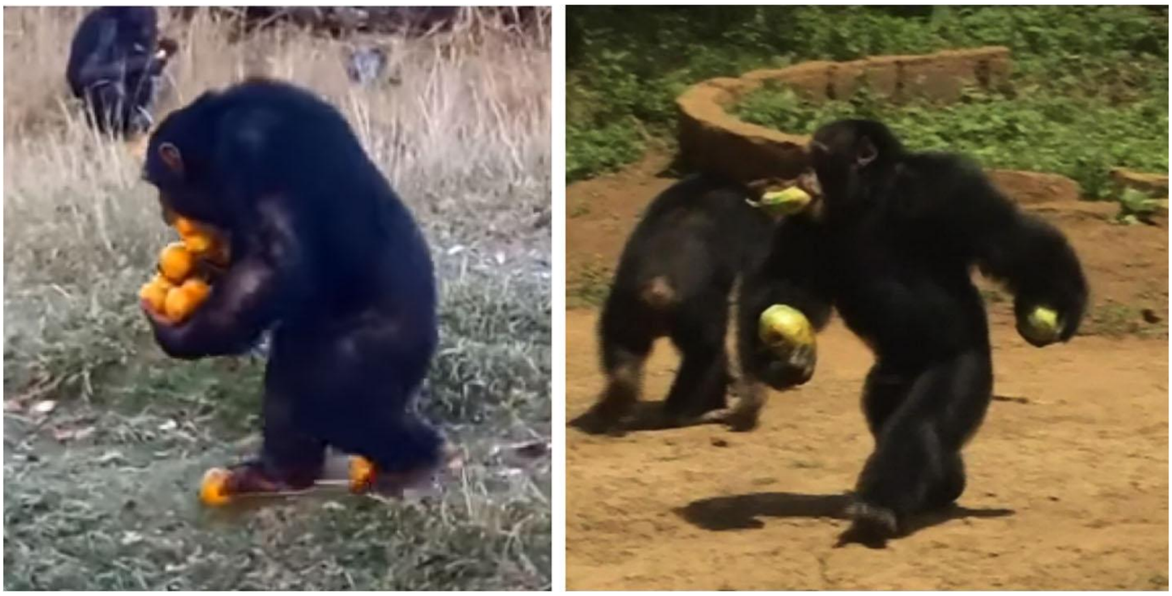

Fig. 7 Images of chimpanzees walking upright, carrying food items. Why does the chimp walk upright? Does his behavior improve his chances of survival and reproduction under the current conditions, compared to the individuals around him who do not engage in this behavior? Does his behavior change *his body,* or *his genes*? Sources: Carvalho et al. (2012), Fig. 1B, used with permission) and LAFFTRIP Videos (2016)

enabling the behavior of upright walking in a population. Figure 8 shows how a causal map can be constructed and used to discuss and reflect on the factors and causal relationships that may be at play in a population of chimpanzees in which the environment induces upright walking, but may currently not provide strong selection pressure for this behavior, thus not leading to changes of bodies and genes on the level of the population. Specific reflection questions can probe for student understanding of the causal role of each factor (environment, behavior, body, genes), including the role of function and heritable variation, for example:

- Could the behavior of upright walking in a population alone (possibly similar to the one observed in the chimpanzee), without a pronounced relative advantage for survival and reproduction, lead to the natural selection of this trait?
- Could the behavior of upright walking alone (possibly similar to the one observed in the chimpanzee), without differences in this ability within the population, lead to the natural selection of body features that facilitate upright walking?
- Could differences in bodily abilities for upright walking lead to the natural selection of these features, even if they were not influenced by genes?
- Could a genetic mutation alone, without the organism carrying out the behavior of upright walking, lead to the natural selection of body features that facilitate upright walking?

Such "What would happen if" questions are known as counterfactuals in the literature on causation and causal reasoning (Pearl and Mackenzie 2018), and they are important tools to uncover necessary and sufficient causes for a phenomenon.

How does this scenario of chimpanzees walking upright compare to the possible scenarios of the evolution of upright walking in our ancestors? Carvalho et al. (2012) note that, over the

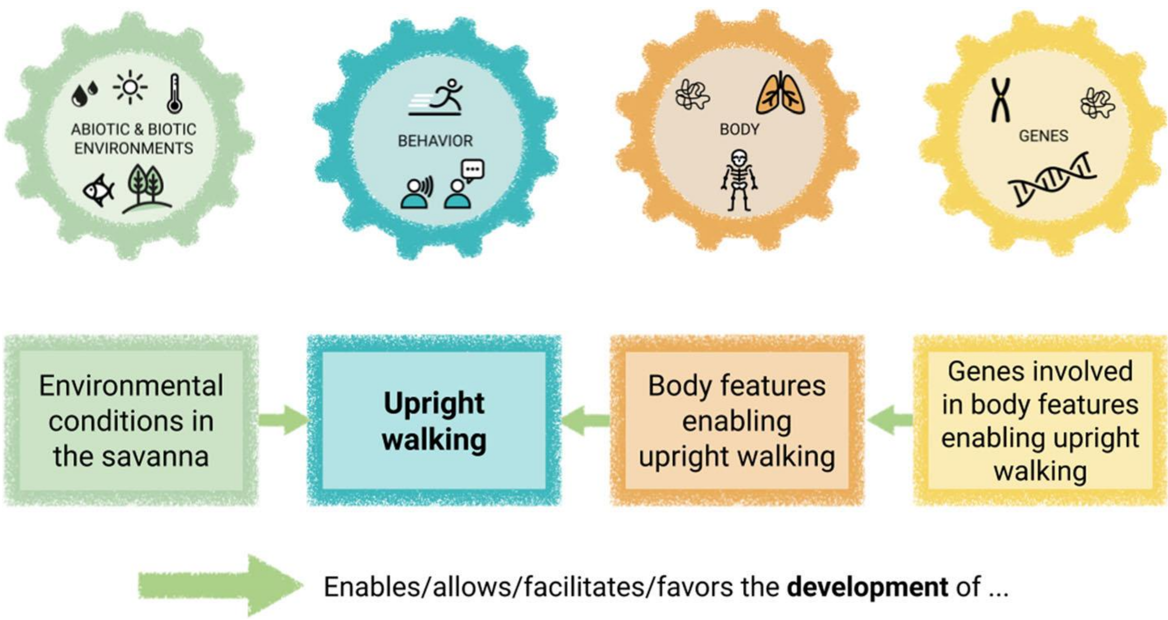

Fig. 8 Causal map of a population of chimpanzees walking upright under certain environmental conditions that elicit this behavior. (1) Environmental conditions may provide more or less strong stimuli for the behavior to be expressed in the population. Assuming that bipedalism does not (yet) have strong consequences on relative fitness of chimpanzees, there would be no significant selection pressure on this behavioral trait, and no selection of other traits favoring this behavior. Current body features of chimpanzees (2), and genes involved in the development of such body features (3), enable the behavior sufficiently well, but their variation in the population would not change further through natural selection

long term and under prolonged environmental selection pressures, "such *carrying of valuable items could act as a strong selection pressure*. The energetic intake resulting from resource monopolizing through short bipedal bouts of carrying *may eventually select for a gradual anatomical change*.", and that "if the environment of early hominins provided similar high value, unpredictable resources at a greater frequency than seen in most of today's chimpanzees, this *could reward higher frequencies and/or longer distances* of bipedal bouts of carriage, creating a *selection pressure for more economical bipedality*." (Carvalho et al. 2012; emphasis added). These quotes highlight how the notion of *behavior as selection pressure* needs to be employed if we want to understand the evolution of a trait complex such as upright walking (which includes behavioral, morphological, and genetic components).

We can represent this in a causal map by adding these "selection pressures for more economical bipedality" (Fig. 9). Under the environmental conditions faced by our ancestors, there was presumably a pronounced selection pressure for the behavior of upright walking, meaning that those engaged in upright walking had a clear fitness advantage over those that did not. The behavior of upright walking would have spread in the population (possibly by a combination of different selection and inheritance mechanisms, such as imitation of others, triggering of the same behavior in individuals independently, and/or differential survival and reproduction). Among those engaging in upright walking, those with body features enabling

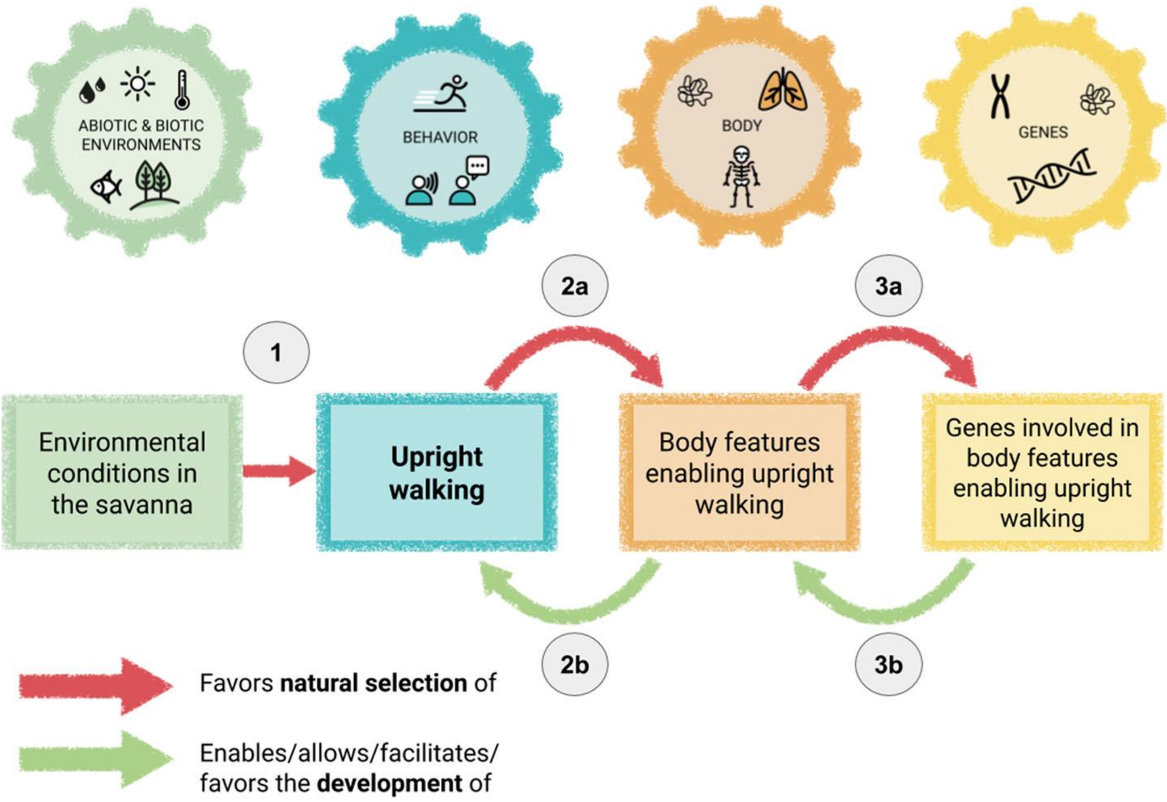

Fig. 9 Causal map of the evolution of upright walking in our hominid line through the interaction of environmental conditions, behaviors, bodies, and genes. (1) Environmental conditions provide a selective advantage to the behavior of upright walking. The behavior would become more frequent in the population. (2) Among the population of increasingly habitual bipedalists and with continuing selection pressure, those with body features enabling better or more efficient upright walking would have had a selective advantage and thus have higher chances of survival and reproduction over others, and those body features would become more frequent in the population. (3) Among those with body features enabling better upright walking, only those whose body features are influenced by genetic makeup would have offspring who have genetically inherited these traits and the resulting selective advantage. Genes involved in bodies capable of upright walking would become more frequent in the population (through differential reproduction and genetic inheritance)

them to do so better, or longer, or more efficiently, would have had a further fitness advantage over others. In this regard, studies that evaluate the energetics of chimpanzee and human bipedalism (e.g., Sockol et al. 2007) add important insights into this link of the causal chain, i.e., the role of body features enabling or facilitating upright walking. Among those with body features that improved upright walking abilities, only those whose body features were influenced by their genetic makeup would have offspring that would have genetically inherited these traits and the resulting fitness advantages. Genes involved in the development of body features that promote upright walking would have spread in the population through differential reproduction and genetic inheritance. Thus, in this causal map of the evolution of upright walking, together with population thinking prompts that highlight the role of population-level variation within each factor, we have explicitly integrated and closed the loop between "need" and "natural selection," as well as between proximate mechanisms (behaviors and preferences in response to environment) and evolutionary consequences.

As a side note to causal mapping, it is important to point out to students that such causal maps of complex biological interactions are never necessarily "complete," but provide a snapshot of theoretically important interactions that we are concerned with in a particular inquiry. In fact, an additional valuable reflection on the development of the phenotype of "upright walking" can be a question about the possible role of social environment. Humans do not begin to walk upright soon after they are born. Instead, they learn this behavior over the course of their first year (Fig. 10).

What role might the transmission of the behavior by *social learning* and *teaching* play in the development of this phenotype? Would a baby learn to walk upright in the same manner, if no other human around him did so, or if no other human was supporting him or cheering him on in his attempts to stand up, thus reinforcing the behavior? We cannot find out by conducting an experiment for ethical reasons, but observing the way that parents and others as well as

Fig. 10 Videos of human children learning to walk upright can be a valuable tool for reflection on the different resources (beyond genes) that may play a role in the development of the behavioral phenotype of upright walking. Source: rbtha (2012) https://www.youtube.com/watch?v=jIzuy9fcf1k&t=

cultural objects in the environment support the developing human in learning this behavior can give us a clue that perhaps the social and cultural environment may indeed play some role in the causation or *developmental reconstruction* (sensu Oyama et al. 2001) of this phenotype. One opportunity to reflect on the causal role of the sociocultural environment regarding the development of human locomotion is provided by the study of child motor skill development across cultures. Studies find that there is substantial cultural variation in the onset of various stages of motor skill, apparently due to "cultural and historical differences in childrearing practices and infants' everyday experiences" (Rachwani et al. in press; see also Karasik et al. 2010).

Another opportunity to reflect on the causal roles of genes, body structures, brain function, and sociocultural environment regarding the development of human locomotion is provided by observations of human individuals who have apparently not developed the capacity for walking upright but instead habitually walk on hands and feet, the so-called Uner Tan syndrome. Scientists debate around the role of genes and other factors in the development of this phenotype, but there seems to be some agreement that it involves complex interactions among a few genetic mutations that influence brain function, constraints, and opportunities provided by evolved human body features, as well as factors in the social environment of these individuals (e.g., Humphrey et al. 2005; Shapiro et al. 2014; Tan 2010; see Online Resource 4 for classroom discussion ideas on these aspects).

How can we add these additional causal factors, specifically of social environment, into our causal map? Figure 11 shows the modified causal map to indicate the possible causal role of social environment in facilitating the development of upright walking behavior.

Such explicit considerations of other causal factors beyond genes can support transfer of learning and assessment of student understanding as well as the cultivation of a more

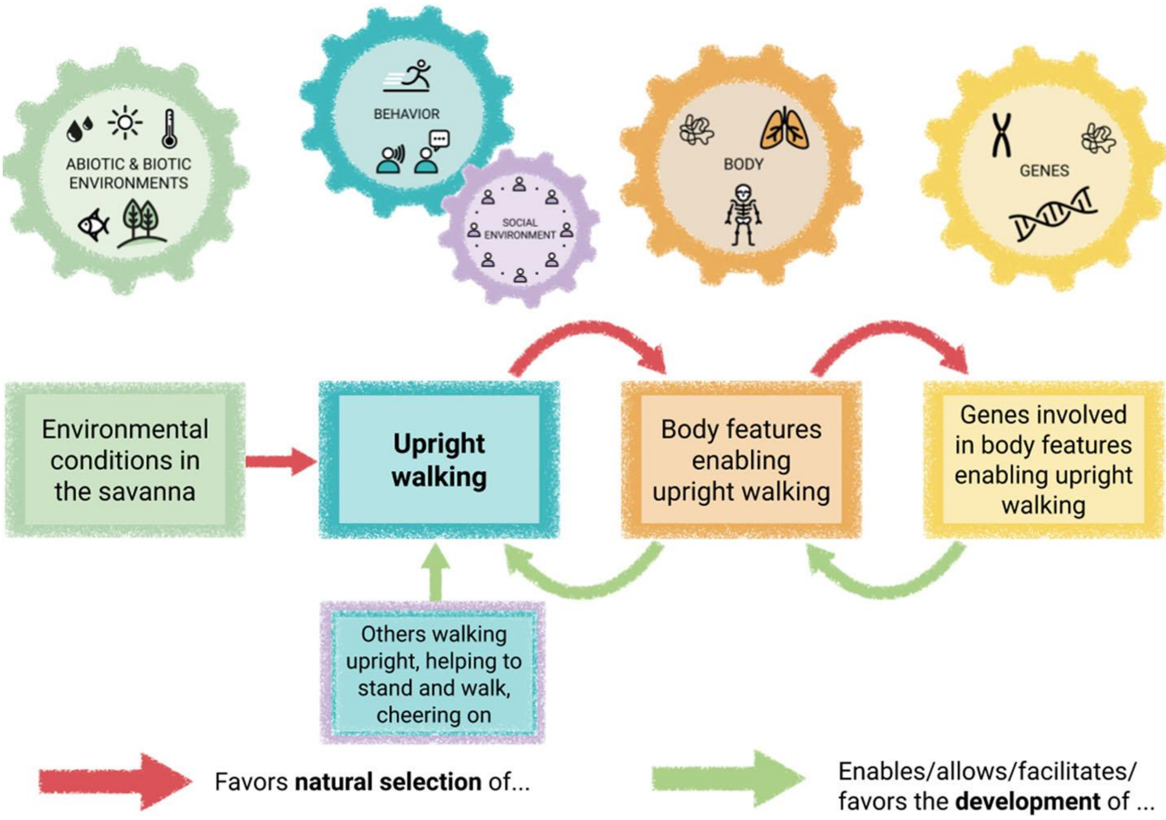

Fig. 11 Causal map of the evolution and development of the phenotype of upright walking with the additional causal role of social environment

decentralized mindset about the emergence of phenotypes (see Jamieson and Radick 2017; Oyama et al. 2001).

Such causal maps can become sequentially more complex if we include more traits, including cognitive traits, that are thought to have emerged during *Homo* evolution, such as meat-based diet, cooperative foraging, tool use/toolmaking, social temperament, social cognition, social learning and teaching, communication, cognitive skills, and brain size. Figure 12 shows a possible causal map that links all of these traits. Note the feedback loops—an important concept in systems thinking—that can be pointed out to students in such a map. Note also that there are still many more conceptually correct causal arrows that could be added to this map. Furthermore, the question whether a certain trait has undergone selection because of a specific function (e.g., whether upright walking was selected because it facilitated tool use, in addition to other functions) is an empirical one that is often difficult to investigate precisely because of the complex nature of causation during evolution, and causal maps can help clarify and reflect on this fact (e.g., Should we add a natural selection arrow or not, from tool use to upright walking?, see Fig. 12). We argue that it is productive to discuss with students the tentative and incomplete nature of these models, as well as the complexity of finding answers to these questions, as these are precisely the questions that evolutionary biologists engage. The function of the nose in holding glasses is an often cited example in which it is easier to see that the nose has not been selected for this function, thus does not exist because of this function. However, sometimes we do not know enough to decide whether a trait exists because of a particular function (i.e., has been selected because of it), while a particular function may nonetheless be of biological importance to an organism. Exaptation is a concept used in evolutionary biology that describes this notion of traits serving functions for which they were not selected. This issue relates to the problems around teleological reasoning pointed out previously, namely that student reasoning about ecological relationships involving functions may reflect valid biological reasoning, rather than an instance of faulty teleology (Ojalehto et al. 2013).

4 Considerations for Classroom Implementation

In this section, we highlight a few theoretically informed educational design considerations for the use of the causal mapping tool in classroom settings, based on the theories and methods of conceptual understanding (Stern et al. 2017), conceptual change (Kinchin 2000), cognitive load (Clark et al. 2006), transfer of learning (e.g., Haskell 2000; Kurtz et al. 2013), and use of concept maps in education (e.g., Novak and Cañas 2004, 2006; Roth and Roychoudhury 1994; Schwendimann and Linn 2016). We focus on the theme of human evolution, but note that the causal mapping tool can be used in evolution education more generally across a range of species and traits.

1. *Scaffold the introduction of the causal mapping tool on a trait-by-trait basis throughout a unit on human evolution.* Start with traits that can be easily observed such as morphological features in fossils as well as extant humans and nonhuman primates, or observable behaviors in extant humans and nonhuman primates such as locomotion. Especially in human evolution, the trait of upright walking (see section above) is a good starting point to introduce the causal mapping tool and methods of evolutionary anthropology, as this trait is generally considered to be among the first to change since the split of our lineage from

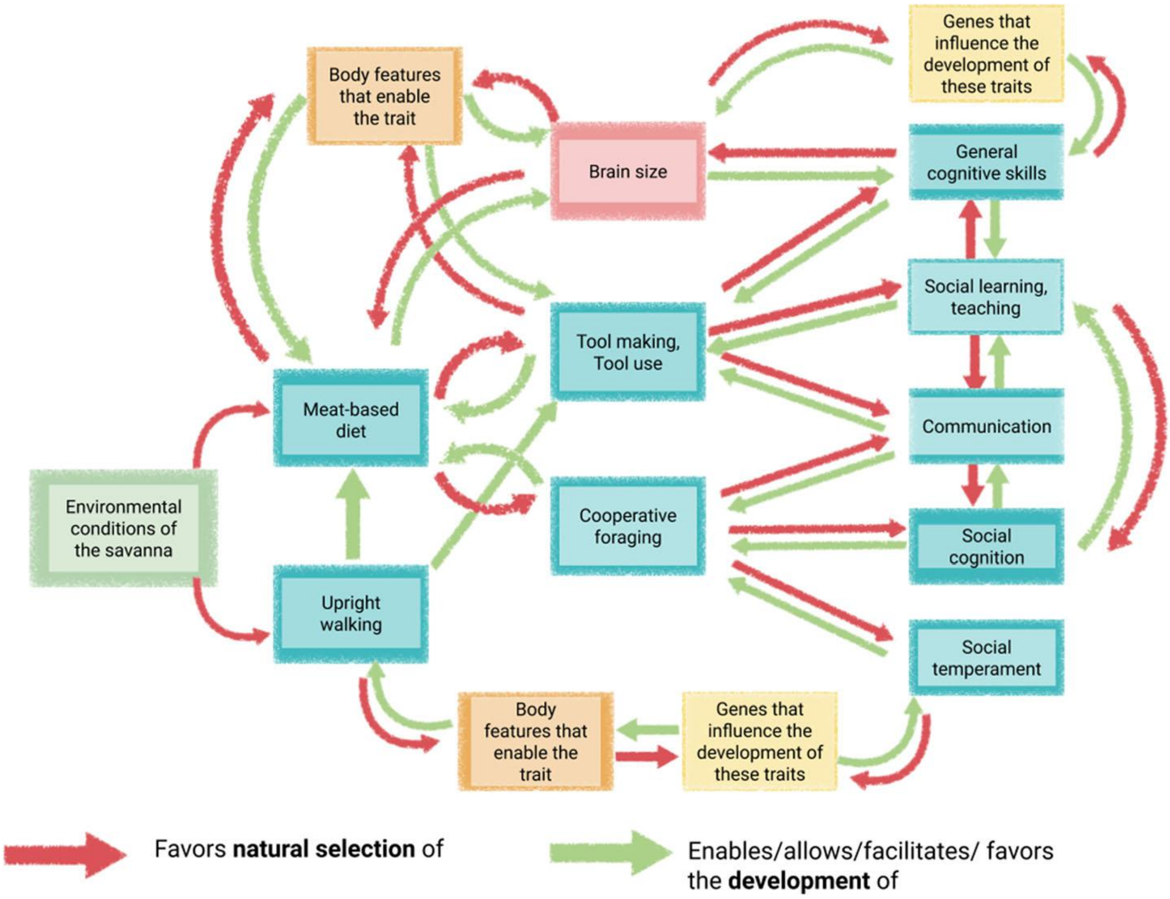

Fig. 12 Causal map showing some of the possible causal linkages that lead to the natural selection and development of various traits during the evolution of the *Homo* lineage. Note the feedback loop between meat-based diet, toolmaking, cognition, and brain size

the last common ancestor with chimpanzees. It is also linked to easily observable evidence in the fossil record of changes in morphological traits that seem to be linked to this behavior.

2. *Engage students in the phenomena of trait change over time.* Provide students with diverse materials (images, fossil replica, observational and experimental data, texts, videos, etc.) that let them explore and discover a change in the focal trait or set of traits over human evolutionary history. If relevant and appropriate, provide students also with information about the environmental conditions during this same time, and/or about the possible functions of the trait under these conditions.

3. *Elicit initial student conceptions.* Prompt students to describe initial ideas about why and how these changes in traits might have come about over time. Identify possible misconceptions and highlight important terms and elements in student answers such as the terms adaptation, environmental conditions, and better survival. Terms related to causal domains (see Fig. 5) like “environment,” “body,” “behavior,” and “genes” can be used to introduce students to the respective causal domains. Terms related to causal relationships such as “the environment leads to” and “it changed the body” can be used to introduce students to the causal arrow. The teacher might further probe student thinking by asking questions such as “But how exactly does the environment lead to changes in the body over time?” Depending on students’ prior knowledge, this can serve either as an introduction to the

mechanism of natural selection and the related concepts of fitness and inheritance (see next point), or as an opportunity to assess student understanding of these concepts.

4. *Introduce students to, or review, the mechanism of natural selection.* This can be done, for example, by using the Natural Selection Worksheet (see Online Resources 1 and 2 as examples for upright walking and cooperative foraging), with which they calculate and graph the changes in trait frequencies in a hypothetical population. The resulting graph can be used as an icon to remind students of this population-level sorting mechanism. Let students describe in their own words what natural selection means based on the completed worksheet. The teacher can then introduce the type of causal arrow denoting "natural selection of" in the causal map, possibly in combination with the population graph (see Fig. 3, Online Resource 3).

5. *Model the construction of a simple causal map.* Teachers should demonstrate the construction of an initial simple causal map regarding the focal trait together with the class, using only a few concepts. A handout introducing the causal mapping tool might also be provided to students before or after (see Online Resource 3).

6. *Scaffold more complex engagement with causal maps.* Provide students with variously scaffolded materials throughout the unit on a range of traits, from completing elements in an "expert skeleton map" (a worked example or partially completed causal map), to constructing maps from a list of given items and to constructing causal maps from scratch (Clark et al. 2006; Novak and Cañas 2004, 2006). Students can also "translate" narrative accounts of trait evolution into causal maps or vice versa.

7. *Maximize reflection and social learning.* Students should initially work in groups for the construction of causal maps (Novak and Cañas 2006), and student groups can be asked to share and compare their causal maps, or compare them to an expert map, critique each other, propose further arrows and concepts, and correct conceptually incorrect arrows (Schwendimann and Linn 2016).

8. *Cultivate transfer of learning.* Provide students with opportunities to practice and apply causal mapping across a number of sequentially more complex traits (Stern et al. 2017). To this aim, we have continued to produce causal map "vignettes" for a range of traits and themes in human evolution, which can help to scaffold and transfer the causal mapping method throughout a unit on human evolution, from upright walking to more complex themes like adaptations to group life, to the complex causal relationships that continue to shape the cultural evolution of our species in the present and future (see Online Resources 5 and 6 and Fig. 12 as an example of an emerging causal map involving a range of traits).

9. *Emphasize the tentative and partial nature of causal maps.* Highlight to students that such causal maps are never quite "complete," but merely useful models, and that biologists use such models to identify and disentangle the multitude of factors that may play a role in the evolution and development of particular traits of interest, in humans and other organisms. In higher grades, the teacher might show to students examples of causal maps produced by scientists to emphasize this point (e.g., Antón and Josh Snodgrass 2012; Chudek and

Henrich 2011; Coward and Grove 2011; Koops et al. 2014; Laland et al. 2011; Whiten and Erdal 2012).

10. *Formative or summative assessment of student causal maps.* Utilize methods developed for the use and assessment of general concept mapping techniques in education (e.g., Cañas et al. 2004; Liu and Lee 2013; Van Zele et al. 2004). For example, student-generated causal maps can be assessed and compared by the number of concepts used (including from a provided list of concepts), by types of causal arrows used (both types or one type, whether there is a legend denoting the meaning of arrows), and by the number of conceptually wrong connections (wrong type or wrong direction; see above). Some connections might also require further elaboration. For example, if a link is produced from "meat-based diet—selects for—genes involved in the development of this trait," it is unclear which gene(s) for which trait(s) students might be considering in this case. Students can therefore be prompted to think about possible mediating phenotypic traits (body, brain, behavior) in this causal chain. Connecting causal maps with student written explanations may help to further elucidate their reasoning. Teachers can further probe for student understanding of the causal roles of each factor using reflection questions highlighted in the previous sections.

5 Considerations for Further Research and Development

The implementation and further design of the causal mapping tool presented in this paper is part of a long-term *design-based implementation research* (DBIR; Fishman et al. 2013; McKenney and Reeves 2018; Penuel and Gallagher 2017) project by the authors (Eirdosh and Hanisch 2020). The aim of the project is to develop teaching tools and lesson materials as well as training and guidance for teachers and curriculum coordinators to integrate innovative methods and insights about human evolution and behavior into educational practice across subjects and educational contexts. This is achieved through coordinated efforts in documenting and evaluating the implementation of educational innovations across a diversity of contexts, such that higher-level design features and guidance for local adaptation emerge.

Toward this aim, we have begun to collect illustrative case studies of the implementation of this causal mapping toolkit in German high school biology classrooms (see Online Resource 7). These case studies indicate that the use of causal mapping, in combination with other tools that cultivate population thinking, can yield productive classroom discussions and allows assessment of student understanding in various ways, often with greater depth and nuance than through classic misconception questionnaires. Furthermore, students were able to understand and apply the causal mapping technique, including the meaning of the different causal relationships, after minimal instruction and minimal previous exposure to concepts in evolutionary biology and anthropology. Within our open, collaborative DBIR project, we will continue to support the development and evaluation of teacher training and instructional guidance to enable teachers to flexibly use and adapt the causal mapping method in their evolution classrooms.

Future research in evolution education more broadly may use the causal mapping technique as an assessment tool to assess the variation in individual student understanding, to identify prevailing misconceptions including teleological reasoning and other common misconceptions in evolution education, and to develop further instructional techniques to help overcome them.

6 Conclusions

In this paper, we aimed to draw attention to the educational opportunities provided by an explicit consideration of behavior as a causal factor in the evolution of certain traits. This role of behavioral variation in affecting evolutionary trajectories has been the subject of much discussion throughout the history of evolutionary thought and has attracted new attention in recent decades. Particularly in the realm of human evolution, many traits of concern are linked to behaviors whose emergence cannot be understood by referring to chance genetic mutations alone, such as upright walking, toolmaking, and many other behavioral and cultural traits. We argued that some concerns for teleological reasoning in student explanations may stem from the lack of opportunity given to students to explicitly link behaviors and other proximate mechanisms to the emergence of traits in populations through natural selection. After all, teleological language seems to stem from our everyday experience—as biological organisms—of needs and behavioral responses to needs. We argued that those behavioral responses to perceived needs, or goal-directed behaviors, are important elements in the causal chain leading to the natural selection of morphological traits or genetic dispositions that favor or enable the adaptive behavioral responses to such needs.

We presented a causal mapping teaching tool that has the potential to elicit and expand student understanding about the role of behaviors, body and brain features, and genes as well as the mechanisms of variation and natural selection in the evolution of traits. Such causal mapping may also provide the opportunity to teach about various concepts in evolutionary biology as well as other topics in the biology curriculum in an integrated fashion, and has the potential to cultivate a more decentralized mindset about the emergence of phenotypes and adaptations in development and evolution. Future research within our DBIR project aims to delineate further guidance to educators regarding the flexible implementation of the teaching tool and opportunities for student assessment across a variety of evolution education contexts.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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2.5 Contribution 5

Evolving Schools in a Post-pandemic Context

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Hanisch	20%	20%	0%	20%	0%

Evolving Schools in a Post-pandemic Context

Dustin Eirdosh and Susan Hanisch

Abstract The Covid-19 pandemic has required schools and students to radically and immediately adapt teaching and learning processes to more distributed, digital, and home-based learning strategies for an indefinite period of time. This situation provides an unprecedented opportunity for students and teachers around the world to reflect on the purpose and design of schools post COVID-19, particularly on the kinds of school design elements that may best meet the needs of all students and teachers in the future. Before the pandemic emerged, the Community Science Lab at the Max Planck Institute for Evolutionary Anthropology had been developing a student-led effort, the Evolving Schools project, for exploring the everyday cooperation dynamics of teaching and learning within their own school communities. This chapter offers an illustrative case study of this project as a novel approach to student participation in school improvement efforts. By involving a small group of students and teachers in reflecting on their experience of changing schooling practices during the COVID-19 pandemic, as well as in exploring scientific perspectives on human learning and cooperation, a new theoretical foundation for the practical empowerment of students and teachers is framed within the aims of Education for Sustainable Development.

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1 Introduction

Teaching and learning was a central driver of the biological and cultural evolutionary emergence of humans as a species ~200,000 years ago, with the origins of such behavioral capacities likely dating to millions of years prior to that (Sterelny 2012). At its core, teaching and learning among humans is about sustaining and innovating adaptive understandings of the world we are inheriting, in order to shape the world as we might imagine it could be (Fuentes 2017). Relative to this context, formal schooling is a remarkably new feature of humanity (Geary and Berch 2016; Gray 2013; see Fig. 1).

How schools can adapt to a rapidly changing world has been a theme in educational development since at least the origins of compulsory education, and has been just as evident in twenty-first century discourse on school improvement (Bryk et al. 2011; Gray 2013). With the onset of the Covid-19 pandemic, this question became all the more urgent to engage with in an effective manner. International school shutdowns, in various forms, have shown a spotlight on educational inequalities, the challenges and opportunities of online learning, and even on broader questions regarding the purpose of schooling and education itself.

Against this background remains the still more complex question of how education research and education science can or should best engage the grand challenges now facing this sector (see extended discussions in Mintrop 2016; LeMahieu et al. 2017). As education systems around the world clamour towards purportedly effective solutions to the myriad challenges wrought by this pandemic, intuition and real or perceived authority may hold as much clout as evidence in the decision making processes at any given level of a school's organizational ecosystem. Educators need immediate solutions to meet the academic and social-emotional needs of students in the present moment, under dynamically uncertain conditions, while education advocates and activists are keen to leverage this moment towards creating a "new

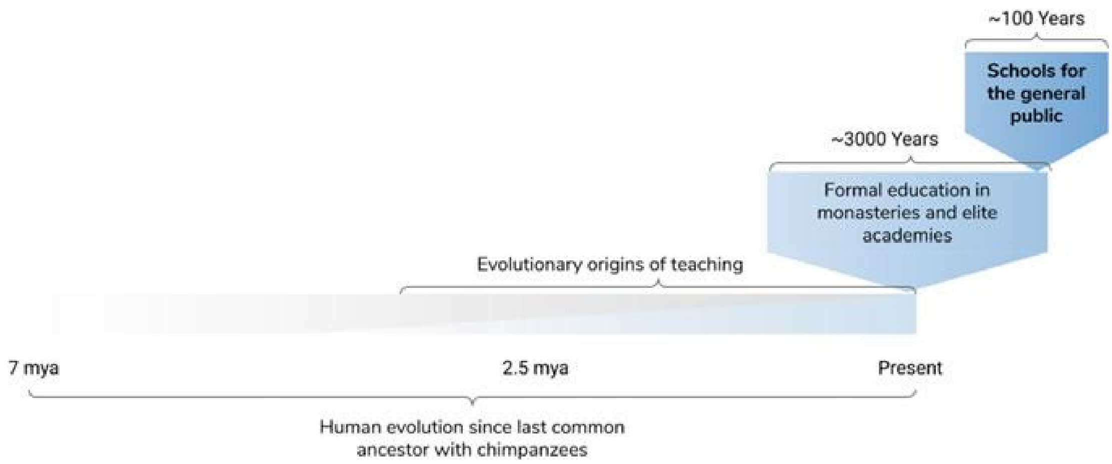

Fig. 1 A schematic timeline of the evolution of teaching and formal education. (Image from the student reading for the Evolving Schools project)

normal", a new understanding of the fragility of past systems and the potential of re-envisioning the potential purposes of education and schooling.

It is remarkably easy to get lost in the noise and needs related to school adaptation processes in the face of this evolving pandemic. Our aim in this chapter is not to offer one more voice advocating for change, nor one more solution purported to address immediate needs. Rather, what we intend to provide here is a minimal yet unique vision for involving school stakeholders in the school improvement process, the *Evolving Schools* project as an example of our *Community Science Lab* model. It is minimal in the sense that it is a project built on highly generalized principles of systems improvement practices, and also in the sense that we can only offer a glimpse at the first four months of this exploratory effort to kickstart a new engine for educational innovation. It is unique in the sense that our approach to stakeholder empowerment is grounded within an emerging interdisciplinary synthesis in the human and educational sciences that is simultaneously pluralistic in the breadth of pedagogical strategies it can engage, and unifying in its foundational perspectives on teaching and learning as a core capacity of the human species.

We begin with a brief overview of the theoretical basis and practical context for the Community Science Lab model developed within our larger *Education for Sustainable Development* project (GlobalESD; www.GlobalESD.org) and the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. We then offer an illustrative case study of our exploratory work in developing the Evolving Schools project with a small team of local students within the Community Science Lab context. This work connects to broader educational discourse on the need for *Networked Improvement Communities* (NICs; Bryk et al. 2011) as an adaptive engine for translating educational science into effective innovation through an explicit focus on continuous improvement. Our conclusions highlight the further opportunities for engaging a global discourse towards driving participatory approaches to school improvement that is simultaneously pluralistic and unifying.

2 Community Science Lab Model Development

Human behavior is at the center of our everyday experience, it has been a driver of our evolution as a species, and it remains a driver of our development as individuals and societies. Despite this centrality in our lives, the place of scientific perspectives on human behavior within the general education curriculum remains elusive. In many ways, human behavior is an implicit topic across traditional subject areas, yet it hardly has a place explicitly, save for the occasional introductory psychology electives offered in some secondary school contexts.

To address the challenge of teaching human behavior as an interdisciplinary theme across the general education curriculum, we have advanced a long-term Design-Based Implementation Research (DBIR, Fishman et al. 2013) project, Global ESD (Eirdosh and Hanisch 2019; Hanisch and Eirdosh 2019), which aims to advance a design concept in *Education for Sustainable Development* (ESD) that integrates concepts across evolution, behavior, and sustainability sciences.

The Global ESD design concept contains a wealth of teaching tools and other structural elements to support educators in embracing interdisciplinary perspectives, yet it is based on three relatively straightforward design principles:

1. Focus on Human Behaviors
   Focus on the aspects and everyday experience of human behaviors relevant to human well-being and sustainable development (eg, prosociality, cooperation, sense of belonging, trust, curiosity and creativity, learning and teaching, empathy and compassion, sense of fairness, perspective taking, flexibility, self-control, goals and values, health, prevention). *Focusing on human behaviors helps students relate to and understand the causes of biological and societal phenomena.*
2. Explore Complex Causality
   Explore and reflect on the many causes and consequences of human behavior and on the complex causal relationships in human evolution, behavior, and social-ecological systems: How do immediate internal and external factors, as well as individual development and evolutionary history, function as causes of human behavior? Why do these mechanisms and patterns of behavior exist compared to other possibilities? What consequences do behaviors have for individuals and their environment, in the short-term and in the long-term? Diverse teaching tools such as causal maps and payoff matrices help in reflecting on these questions. *Exploring complex causality helps students understand and relate causal factors in the emergence of human behaviors.*
3. Teach for Transfer
   Ensure students can transfer understandings to novel phenomena, everyday experience and relevant problems of sustainable development across multiple scales and contexts of global society, with the help of analogies, analogy maps, and other teaching tools. *Teaching for transfer requires the iterative exploration of diverse human behaviors and contexts.*
   Since 2015 we have been developing a database of teaching materials created through teacher development programs and teacher-researcher collaborations in real-world classroom contexts, within this educational design concept. These classroom materials provide usable and pedagogically informed approaches to engaging students in understanding human behavior as an interdisciplinary theme, however, they largely fall within the realm of more traditional classroom learning and do not engage students in the real-world issues of sustainable development. In 2019, through our work with the Department of Comparative Cultural Psychology at the Max Planck Institute for Evolutionary Anthropology, we launched the *Community Science Lab* as an exploratory approach to, broadly, engage students and teachers in understanding and influencing the cooperation dynamics that pervade their everyday lives and which impact local to global

sustainability issues. Building on the Global ESD concept of "reflecting on the everyday experience of human behavior in the light of evolution and sustainability" (Hanisch and Eirdosh 2019), the inaugural year of the Community Science Lab aimed to follow the minimal design principles set out by Global ESD, while empowering and following student voices in the process.

Starting in September 2019, a team of four students from a local 8th grade English class volunteered to visit the Community Science Lab within the institute, for 1.5 h per week. Sessions began by exploring some conceptual foundations in human behavior across evolutionary, cross-cultural, developmental, and sustainability contexts. Given that the student participants were engaged members of their local *Fridays for Future* climate action school protest group, our team (led by student decision-making) decided to focus on trying to understand the cooperation dynamics in this context.

Building on the international *Prosocial World* research program (Atkins et al. 2019), we engaged students in understanding the *theory of collective action* originally developed by Nobel laureate, Elinor Ostrom, as a democratic framework for understanding the *core design principles* associated with effective group cooperation across diverse contexts and levels of social organization (Ostrom 1998; Poteete et al. 2010; Wilson et al. 2013). Informed by this theoretical framework, students and lab leaders developed a short survey focusing on various stakeholder perceptions regarding the purpose and efficacy of the *Fridays for Future* climate action school protests. While some stakeholders in the *Fridays for Future* movement espoused an "us versus them" mindset of movement supporters versus opponents, the student-led survey tentatively revealed a more complex picture. Students gained insights from this educational project suggesting that many supporters of the movement (students, teachers, and parents) also harbored significant critical views of some aspects of this activism. Likewise, many stakeholders claiming to be critical of the movement often described significant aspects which they supported and valued.

In discussing next steps with our student researchers, we identified challenges in further elaborating research within the *Fridays for Future* movement, namely that the decentralized structure of the movement made it challenging to further elaborate the study with significant community buy-in. Simultaneously, we also explored further the *root causes* of the movement itself. While *Fridays for Future* is ostensibly about action on climate change, our students were keen to elaborate that it is also about the purpose of school itself, and a perception among students that current school practices are not empowering them with the knowledge and skills needed to tackle the grand challenges they will clearly face in their adult lives. Against this background, and with a student vote, we decided to shift emphasis into understanding the cooperation dynamics within schools themselves. This occurred in the first week of February 2020, just prior to a planned ~6 week break, both to allow students time to engage their final exams and enjoy spring break, as well as allow our team to plan the upcoming semester within the context of this emergent focus on school culture.

3 The Evolving Schools Community Science Project

During this ~6 week break in the Community Lab sessions, our team developed a plan for the *Evolving Schools* project, as a means of both going deeper into the evolution science perspectives on teaching, learning, and human cooperation, as well as to elevate student voice within school improvement discussions by empowering them to use more advanced methods from the Prosocial World research program.

We were able to have one inaugural project session at the Max Planck Institute in mid-March prior to the full shutdown of schools and our institute in late March. We present here a brief overview of the project as planned, a summary of the challenges faced during implementation within the pandemic context, and highlights from the collaborative project report produced from this work.

3.1 Project Overview

The central aim of the Evolving Schools project was to develop a model for authentic student engagement in the improvement of school culture through project-based conceptual learning about the science of learning and culture. That is, we sought to empower our students to elevate their voice as drivers in the cultural evolution of their school, while using these empowerment processes to drive academic learning in the sciences of evolutionary anthropology itself.

We developed this idea broadly within the Global ESD design concept, and specifically building on the emerging pedagogical knowledge synthesis occurring in the field of *conceptual learning* (Cope and Kalantzis 2015; Stern et al. 2017). Towards these aims, we began by structuring an overarching research question and several student facing questions. Within this direction we then drafted some student readings to engage and elaborate student conceptions in relation to scientific perspectives in the evolution of teaching and learning, and outlined a Project-Based Learning protocol adapted from Stern et al. (2017, p. 80).

3.2 Research Questions

The *Evolving Schools* project is conceptualized as an education project aiming to empower students as community scientists, and as such, has been structured around a guiding question for educators and project coordination partners, as well as several student facing questions (Table 1).

Table 1 The essential questions driving the planned *Project-Based Learning* protocol for the Evolving Schools project

Guiding question	What learning potential and challenges exist in engaging students in evolution science perspectives on teaching, learning, and school culture?
Student facing questions	What conceptions do school students have regarding the purpose and autonomy of their learning experiences [esp. during the pandemic as it relates to normal school contexts]?
	What conceptions and questions do students have regarding the diversity of learning theories for the design of school curricula?
	Can the collective conceptions of students on these issues inform educational policy and design discussions?

3.3 What is Meant by "Evolving Schools"?

An important clarification should be made regarding our choice of the project name *Evolving Schools*. The concept of evolution is used in a wide diversity of ways across various scientific disciplines as well as within popular culture. In biology, evolution can variously refer to changes in the frequency of genes within a population, or more generally, to changes in the frequency of heritable variation of traits in a population. In evolutionary anthropology, the conceptualization of evolution has been generalized to include changes to the complex systems that enable the retention or reconstruction of behavioral, cognitive, and cultural traits (see Table 2; Hanisch and Eirdosh 2020 for an elaborated discussion).

How diverse scientists conceptualize evolution, and how scientists relate these diverse conceptualizations to practical implications for school design remains controversial. Indeed, it is exactly this controversial space in which we wanted to engage student reflection and voice.

Given that our 8th grade students had not yet had significant instruction in evolution science, we crafted a four page reading that framed a simple historical context for the origins of modern schooling, and offered three different narrative perspectives. We summarize these perspectives below, however the full student reading can be found within the Evolving Schools (2020) project report.

3.4 Three Perspectives on Evolution and Education

Perspective 1: Students should learn like our ancestors evolved to learn

Humans have been teaching and learning from each other for millions of years, therefore we are genetically adapted to learning in certain ways. By studying how small-scale hunter-gatherer communities engage in teaching and learning we can identify important aspects of how modern education should be designed. For example,

Table 2 An analogy map comparing evolutionary concepts across domains of genetics, learning, and culture

Concept, process, principle	Genetic evolution	Cognitive-behavioral evolution (learning)	Cultural evolution
What is the relevant level of analysis?	Populations of organisms in an ecosystem	Populations of concepts, mental models, and behaviors in an individual	Populations of individuals and groups exchanging information
How is variation of traits caused?	Putation, 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 selection 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 (*natural selection*); greater reward, appeal or attractiveness of the trait (*cultural selection*)
How are traits inherited, transmitted, or retained?	Biological reproduction, mitosis/meiosis	Encoding into long-term memory for later retrieval	Social learning/imitation, teaching; technologies and infrastructure that endure

In this context, schools are immensely complex evolving ecosystems of individual and social learning processes. To the degree we can clearly define the goals of education as a whole, and for specific schools in particular, we can begin to think about the social conditions that will favor or hinder the characteristics of these systems that we value most

students should have unlimited free time to play with the tools of the culture in a community of helpful supporters, rather than being tested according to a pre-set curriculum.

Perspective 2: Teachers should help students evolve their minds

Humans have been teaching and learning from each other for millions of years, therefore we are genetically adapted to engaging with the tools of the culture we are born into. However, through cultural evolution the world that we live in today is drastically different from the world that our ancestors lived in, therefore we need new tools and knowledge about how to learn best in today's world. Because the tools of modern societies include complex ideas and concepts we would not have encountered in our evolutionary past, it is the role of teachers to use modern teaching practices to evolve new species of thought within the minds of students.

Perspective 3: Students should be empowered to evolve their own education system

There are aspects of Perspectives 1 & 2 that are correct, but neither one is fully adequate to design modern schools that are enjoyable and effective for all students. Instead of choosing one perspective or the other, students themselves, with the help of teachers and scientists, should understand the evolutionary science of learning and be empowered to evolve their own school system to be most enjoyable and effective in their own communities.

3.5 *The Project-Based Learning Protocol*

In order to structure the investigation, we adapted the Project-Based Learning (PBL) protocol from the *conceptual learning* approach of Stern et al. (2017, p. 80; see Table 3). This model provides a clear roadmap for project development while integrating best practices in teaching for conceptual understanding. Such an approach aims to

Table 3 Planned project-based learning protocol for the evolving schools project

PBL protocol	Evolving schools project plan
1. Project launch	• Discuss project aims • Engage students in student reading on perspectives in the evolution of teaching and learning • Reflect on core concepts and conceptual relationships in the readings
2. Help students plan inquiry and build background knowledge	• Engage students in peer reflection and thematic analysis on their interpretations of the student reading • Identify areas of agreement, disagreement, or interest for further investigation among their peers • Plan community science investigation(s)
3. Monitor student inquiry processes and guide student reflection	• Support students in the development and implementation of their community science investigations
4. Support students as they construct high-quality products through critique and revision	• Use Community Science Lab weekly sessions to engage students in peer reflection and rubric-based analyses of their emerging research products and final project report
5. Organize students to present or publish their final products to a real-world audience	• Support students in the publication and community presentation of the Evolving Schools report
6. Provide opportunities for reflection on the process	• Final reflection session • Planning for project continuation in the following school year • Celebration

weave student learning across a multitude of pedagogical approaches, including conceptualizing, experiencing, critical analysis, and creative design (sensu Cope and Kalantzis 2015).

3.6 Challenges Within the Broader School Adaptation Context

Immediately following the project launch session, the Covid-19 situation in Germany (and across the western world) escalated at a dramatic rate. School closures occurred in Leipzig by the end of March, and the fate of our project (and of student learning as a whole) was suddenly put into an unknowable jeopardy.

To proceed in this landscape of uncertainty, we began to work in closer partnership with the teacher coordinator at our partner school. This teacher had previously been largely supporting the logistics of engaging our student lab members at the Max Planck Institute, but now served as a critical point of information and process reflection on if and how we might proceed. We agreed to let student interest drive any possible continuation of the project. Within the first couple of weeks of school shut down, our students reported significant stressors, both from the general uncertainty of the pandemic situation, but as well, from a relative lack of coordination in the approach and clarity of expectations across teachers in navigating how student learning should best be supported. Teachers, for their part, also reported a state of stressful chaos as they got limited and sometimes conflicting guidance from higher levels of leadership. Despite this stress, our core student group decided they did want to continue to try to engage through virtual collaboration, albeit somewhat reduced.

To account for the multiple limitations imposed by this lack of direct classroom engagement, we crafted a set of adapted research questions and project processes that focused more on capturing and reflecting on student voice, and less on students as direct drivers of community science investigations.

We outlined two simplified research questions:

1. What are student conceptions of current debates in the evolutionary anthropology of modern education systems?
2. What are student conceptions about the possibility of elevating student voice in the ongoing cultural evolution of modern education systems?

The process adaptation included working with our teacher collaborator to also offer the project to the 10th grade class, from which ($n = 29$) students volunteered to engage. Due to the challenges of inconsistent IT access for students, we adopted an asynchronous online learning plan. In this context, a combination of YouTube videos, student essays, and iterative video/questionnaires based on thematic analysis of their essays provided a set of mechanisms to drive the conversation forward based on student voice, while also minimizing additional stressors on student work load. These methods also served as our primary source of data collection.

Our teacher partner has a strong interest in student well-being and the role of student voice in schools. Throughout this process, and during the final project reflection interview, she repeatedly voiced concern about the lack of clear and coordinated guidance leading to cooperation dilemmas among teachers in regards to developing adaptive innovations during this time. That is, in the face of unclear expectations, varying teachers had varying responses. Those teachers who adopted a view that normal school work and grading expectations would simply be ported to online contexts created demands on students' time and skill sets that, in essence, hindered students' ability to engage potentially more valued opportunities regarding social-emotional learning, self-care, and other activities designed to support students in the self-reported challenges of stress and anxiety many of them were facing.

Against this challenging background, our continuous engagement with ($n = 33$) students throughout the remainder of the school year speaks to their motivation and interest in advancing student voice within the scientific framework offered by this project.

3.7 The Evolving Schools Report

While the original project plan suggested the project report would be fully student driven, the adapted version, edited by us, still captures and highlights a wealth of student voices within the core theoretical framework. The full report is available at the project website (https://EvolvingSchools.GlobalESD.org), our intent here is only to highlight three key findings relevant to our discussion on next steps for the project.

First, through student reflections on their conceptions of what is meant by the concept of "Evolving Schools", we were able to identify that, while they collectively hold a diversity of ideas about what this phrase means, there is a wealth of scientifically adequate thinking as it relates to modern perspectives in cultural evolution science. That is, even without instruction, students' intuitive, popular conceptions of "evolving minds" and "evolving schools" contains kernels of scientific conceptions that could be developed with further opportunities for engagement. Importantly, because the dynamics of cultural evolution are both similar to, and in some regards, different than, biological evolution, some of these student conceptions stand in contrast to the understood aims of evolution education within the biology classroom. We discuss these important conceptual overlaps and divergences at length in our article collection on *teaching evolution as an interdisciplinary science* (Hanisch and Eirdosh, in press). Critically however, students tended to have a non-trivial and partially scientific understanding of the complexities of cultural evolution science within this context, and reportedly did not find this view in contrast with their understanding of biological evolution.

Second, students overwhelmingly preferred perspective #3 (students should be empowered to evolve their own school system), explicitly viewing this as an integration of all of the perspectives offered. There was a high diversity of thinking, especially regarding the specifics of school design policy options, but ultimately students seemed to strive for a relatively nuanced balance between student autonomy (which they deeply value and want more of) and the value of structured learning from expert educators (which many of them also deeply value). Also of note, students tended to reject perspective #1 (students should learn like our ancestors evolved to learn) most often due to a perception that this amount of freedom would not prepare them for the modern world. When we discussed this finding with educators in various *Self-Directed Education* movements (which this perspective was aiming to capture), there was concern that the emphasis on ancestral learning in small-scale societies, while being a theoretical core to *Self-Directed Education*, may have biased student responses. Importantly, while students frequently overtly rejected perspective #1 in their direct response to it, their later justifications of support for perspectives #2 and #3 commonly invoked core elements of perspective #1. Thus, these findings should not be interpreted as an overt student rejection of self-directed education practices.

Finally, while student attitudes regarding the potential of this project to actually lead to school improvements ranged from cynical skepticism about the motives of educational policy makers, to more nuanced optimism, students overwhelmingly agreed the process was useful. In a concluding survey, only one student preferred to not engage in the project next school year, four suggested they would like to stay engaged if they could get a grade for the work, and the remainder ($n = 28$) reported an intrinsic interest in continued project engagement.

3.8 Next Steps for the Evolving Schools Project

Given the strong student interest and conceptual richness of their engagement, we are now planning the next steps to improve the project implementation within our partner school, and also to open the methods and materials to allow for a more networked, collaborative, open science approach to this work.

Improve teaching materials. Having found that students intuitively prefer the third perspective on evolving their own school system, largely because it integrates the first two perspectives, we will make several changes to the student reading. First, we plan to offer only the first two perspectives during the initial reading and reflection phase to better capture students' conceptions of this specific problem space in the learning science literature. Second, because we found students tend to reject perspective one on a perception that it is an outdated mode of learning, we will include more explicit examples of modern school environments and research into their efficacy for student adaptation to future academic and work life in modern societies (e.g. Sudbury school models, see Gray 2013). We are working to additionally develop and curate new resources to help students dive deeper into school culture improvement (see our *Community Science Field Guide for School Culture*; Hanisch et al. 2020) as well as evidence-informed teaching and learning environments (see Hattie 2012; Kirschner and Hendrick 2020). In particular, the in-development *Prosocial Schools Inventory* will provide a roadmap for student–teacher teams to sustain strategic discussion and community science investigations towards school culture improvement over the course of a semester or entire school year.

Adapt PBL protocol for the challenges of pandemic school closures. As of this writing, the Covid-19 pandemic situation remains highly unstable around the world. The state of school opening and school strategies for students in the coming year is unknowable at the moment, therefore we aim to "Covid-Proof" the project protocol by planning for not only in person options, but also strategically improved blended and fully online options. Again, given the known inequities of synchronous online learning (e.g. video conferencing), we will adopt asynchronous strategies as the dominant approach. Key to this model will be social annotation technologies, such as the free online platform Perusall (Miller et al. 2018), which enables asynchronous peer-to-peer collaboration in interpreting and clarifying key readings and videos, while providing strategic analytics on student engagement and understanding to educators. Social annotation can also be used within the *Evolving Schools* project context to quantify student consensus or disagreement on a variety of specific propositions about school design. Combined with short questionnaire, essay, and peer-to-peer chat platforms, we believe a robust engagement with the project can be advanced even within school closure contexts.

Create tools for cross-school collaborations. Because we work within an open education science framework (van der Zee and Reich 2018; Makel et al. 2019), adopting strategies to adapt to the potential challenges of the pandemic has a positive side effect of expanding the potential for cross-school collaborations. In the section that follows, we describe the need and potential to evolve just such a network of schools working towards scientifically informed school improvement.

4 Evolving a Networked Improvement Community

Education science is a richly diverse field, filled both with healthy discussions, and sometimes more tribal disagreements. From an evolutionary perspective, a few things are fairly clear. Our species has been shaped over millions of years by the relatively egalitarian small-scale societies of our ancestors, such that the development of folk understandings of the physical, biological, and social world is a biologically primary capacity of all humans. Over at least the past 10,000 years, ultra-social cultural evolution has radically transformed our social organization many times over, and allowed for the acculturation of a massive store of cultural information far beyond the expectations of our biologically primed capacities for social learning. Schools exist, at least in part, to help bridge that gap (Geary and Berch 2016), on this there is little disagreement. What remains up for debate are the specifics of how to design and continuously adapt schools to achieve this aim in a way that also cultivates empowered prosocial citizens and whole communities. The *Evolving Schools* project was developed to engage students and educators in participatory approaches to bridging this gap between theory and practice. Yet this project alone, especially within the isolated context of individual schools, is unlikely to be sufficient. What is further required is for education science to better engage with long-standing critiques about how we conceptualize and structure our inquiry to support knowledge transfer between research and practice (Bryk et al. 2011; Makel et al. 2019). Many schools have been encouraged to adopt new programs and policies on the perceived evidence-basis for efficacy ("What works") across contexts. The drastic changes that the pandemic imposed in various ways across schools highlights that simply waiting for research to provide that evidence-base is not necessarily an adequate approach to improvement.

We suggest that the recent scholarship on *Networked Improvement Communities* (NICs; see LeMahieu et al. 2017, and the work of the Carnegie Foundation for comprehensive resources on the NIC model) provides the most strategic path forward for empowering schools to adapt and learn from the challenges imposed by this pandemic. That is, schools should adopt new programs and policies on the basis of the actual efficacy *in their context* ("What works, for us, now"). The NIC research model suggests that making educational innovations work in local communities is fundamentally a process of intentional improvement of implementation. Schools need to focus on "getting better at getting better" in implementing the complex processes intended to meet identified aims and serve identified values. Furthermore, improvement is fundamentally strengthened through strategic measurement and networks of social learning.

The challenges that our project team faced in implementing the *Evolving Schools* project during the pandemic were merely symptomatic of the challenges many teachers in that school (and countless schools around the world) were facing. Yet this school has, to-date, no systematic process for improving practice or even understanding the range of valued outcomes from current practices in relation to their pandemic adaptation efforts. How many schools globally are in the same position? The improvements to our project planned for the coming school year represent a small step towards institutionalizing a pathway for elevating student and teacher voices within school improvement efforts, but this work needs to be supported by broader networked improvement work.

For this reason, in parallel with the development of this project, we have expanded collaborations within the Prosocial World research community (Atkins et al. 2019) to launch *Prosocial Schools* (www.ProsocialSchools.org) as an international NIC, focused broadly on improving school culture around valued outcomes. This network is now actively developing toolkits and processes to facilitate an applied toolkit for school improvement that is based on scientific perspectives of the human universal aspects of the cultural evolution of cooperation and learning, while emphasizing community empowerment for local adaptation of core design principles. The *Evolving Schools* project is one approach that more explicitly engages students in the evolution science itself, however the broader Prosocial toolkit can be applied without going this deep into the theoretical framework. By serving as a minimal and uniquely interdisciplinary scientific basis for participatory school improvement, we hope Prosocial Schools can support the improved implementation of Evolving Schools, and a diversity of projects with related aims yet employing diverse approaches.

5 Conclusions

The Evolving Schools project is neither a panacea nor a quick fix solution to the daunting challenges wrought by the global pandemic. Instead, it represents a unique approach to engaging student and educator voices in school change processes through scientific reflection on the adaptive cultural evolution of schools, in a time when reflective, inclusive approaches to change are needed perhaps more than ever. Our illustrative case study does not allow for inference to effective or optimal practices, only a suggestion of the possibility for a stronger integration between academic learning and participatory school improvement efforts. Our modest attempt here to involve students in the evolutionary science human learning as a participatory design exercise was met with enthusiasm and competent reflection even under the most challenging of conditions. Further work is required to empower more educators and students around the world to come together to improve these participatory processes of science-informed school improvement pathways. If networks such as Prosocial Schools can help sustain these broad directions, we could surely evolve new cultural adaptations to the challenges this pandemic has brought, as well as to the many other challenges that the future will inevitably bring, to our educational systems.

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3. Closing discussion

The chapters presented here, taken as a whole, suggest that some dominant traditions within the mainstream of international evolution education research are constraining our collective ability to teach evolution as the interdisciplinary science that it is. That is, significant swaths of evolution education research may be unreflectively *climbing the wrong mountain*, and an intentional change of course is therefore required. Beyond mere conceptual critique, this thesis also offers early glimpses of potential solutions, and hints of what the educational potential of advancing these solutions might be. Critically, the landscape of educational innovation and research needs identified by orienting towards this *mountain of interdisciplinary evolution education* is vast. Any attempt to climb the heights of this brave new world should be made as a team effort, and such teams should be equipped with the tools, information, and skills to comfortably advance to the next highest *resting camp*.

With this aim in mind, I frame this closing discussion around the future directions of this work, within the context of our emergent project, OpenEvo (http://openevo.eva.mpg.de), a digital *basecamp* for climbing the mountain of interdisciplinary evolution education. In line with the educational design concept and research design model described in *Chapters 1.1* and 1.2 (and more extensively in *Appendix B*), OpenEvo uses the world's most widely used open-source Learning Management System, Moodle, as an educational innovation and design research platform specialized in the space of interdisciplinary evolution education.

The sections below outline how OpenEvo builds on the work of this thesis, and in this way, provides a proof-of-concept for the scope and scale of claims made herein. Conclusions then summarize the broader implications of this thesis for the field of evolution education.

3.1 OpenEvo Learning Hub

It is beyond the scope of this section to provide comprehensive documentation of the design details of our emerging online platform, however this section can offer a concise overview of selected key design choices. Launched for selected collaborators in June 2021, the OpenEvo Learning Hub (http://openevo-learninghub.eva.mpg.de) is a dedicated Moodle server at the Max Planck Institute for Evolutionary Anthropology for supporting the evolution of an open, networked, and interdisciplinary evolution education research community.

After an extensive year-long search and analysis of prospective online learning and content management systems, we choose to proceed with Moodle for a number of specific reasons related to our aims. Primary among these reasons are the globally widespread use of Moodle (see https://stats.moodle.org/), the emergence of a socially networked content sharing ecosystem across Moodle servers (*MoodleNet,* https://moodle.com/moodlenet/), and the related commitments to open, collaborative, and ethical platform design (see table 1).

Table 1. The principles underpinning MoodleNet (Source: https://moodle.com/moodlenet/).

Open Open Source. Open Pedagogy. Open Content. Open to all educators to discuss, share and work together to build a better future.	**Transparent** Built in the open, based on suggestions from the community, with MoodleNet you are welcome to observe and participate in what happens behind the scenes.
Safe Secure, standards-based, and GDPR-compliant. MoodleNet communities are moderated by you and your peers, not by a single central organisation.	**Connected** Bringing educators together from around the world, MoodleNet exists to create new connections and strengthen existing ones.
Private MoodleNet is developed using a Privacy By Design approach, meaning you can share as much about yourself as you are comfortable with.	**Ethical** Unlike most other platforms, MoodleNet's business model does not involve selling user data.

OpenEvo is run on a local instance of Moodle, and is working to integrate with the emerging MoodleNet on the basis of these platform design principles. OpenEvo as a platform has therefore also adopted these as guiding principles for future development, in addition to our broader aim of supporting open science across the scientific workflow in evolution education research.

These principles are central to understanding the aims and strategic development of the OpenEvo platform as an international educational innovation laboratory, rather than a static hub for the implementation of predefined online courses. That is, we aim to provide space for scientists, teachers, and students, from all backgrounds and disciplines, interested in collaboratively improving how we teach evolution as an interdisciplinary science.

With this aim in mind, we have structured the platform to specifically facilitate multiple scales of social learning and access to the educational potential within this expansive new landscape. Table 2 provides a quick overview of how the module structure facilitates this multilevel learning capacity.

Table 2. OpenEvo Module structure descriptions.

Module structures	**Description**
OpenEvo Platform Modules	This category includes the core introductory modules for orienting new participants, as well as all stages of users working to learn core skills in educational design (including specific Moodle-based educational design) and community science..
Featured Modules	This category is where scientists and model scientific communities collaborate to evolve featured modules within thematic areas of expertise. All modules here start as draft *repositories* for content area resources. Through scientist and teacher education collaborations, these repository collections can be selectively improved, with positively evaluated materials being copied into *self-study* and/or *instructor-led* modules on this thematic area. All modules can be made more or less open to selected communities or the general public, based on editorial and community-based decision-making.
Field Site Modules	This category is where local communities, typically schools and teacher education groups, anywhere in the world, can develop, adapt, and improve locally relevant resources aligned within the OpenEvo scope. This is a space where teacher education groups can copy, adapt (including translate), and implement featured modules or featured module activities for use in their local university (such modules can be run on the OpenEvo platform or created there and migrated to any local institutional Moodle

	platform, as practical). Additionally, school communities can develop *School Field Site Modules* which can serve as project hubs for evolution-informed community science projects, working towards community-based cultural evolution at any scale of interest locally.

The *OpenEvo Platform Modules* include some basic orientation resources for incoming students, interns, teachers, and scientists. Additionally, this category includes a strategic range of system-level modules (in various stages of development as of this writing), to be made accessible to all system users as core resources relevant across all other module categories. These core modules include the OpenEvo Labs, specifically our Educational Design Lab and Community Science Lab modules.

The *Educational Design Lab* provides resources and activities for orienting to the pedagogical and design research framework for evaluating, developing, and improving content-oriented resources on OpenEvo.

The *Community Science Lab* provides resources and activities for both students and teachers to develop *community science* projects related to school improvement and/or sustainable community development.

As will be described in the sections below, modules within the Featured content and Field site categories on OpenEvo are required to include either an Educational Design Lab and/or Community Science Lab section within the module, which curates or adds specific opportunities for project development related to the module content.

These OpenEvo Platform Modules are being developed to create a smooth and partially automated on-boarding process for motivated students and teachers to use the system tools to optimize their own local learning goals within a shared framework informed by an interdisciplinary understanding of evolution and human behavior. With some basic navigation skills developed in this area, users can proceed to fully engage their target modules. The following sections highlight how featured and field site module categories are being developed to support the networked improvement of resources and curricular plans at different levels within the global education ecosystem.

3.2 Networked improvement of featured content modules

Featured modules represent the highest level of content curation, review, and spread on the OpenEvo platform. Each category within the featured modules category represents a selected *model scientific community* or *thematic area* for module development. *Model scientific communities* represent scientific organizations (projects, networks, institutes, etc) that represent a core area of interest for understanding the full breadth and depth of evolution as an interdisciplinary science (see table 3).

Table 3. *Selected model scientific communities on OpenEvo*. With the aim of connecting current scientific discourse into effective local educational opportunities, OpenEvo is working to support selected *model scientific communities* in developing *content repositories* that pre-service or in-service teachers can explore and improve. As these repositories evolve, it is possible to work towards open access *self-study modules* and various formats of *instructor-led modules*. Collectively, the diversity of scientific disciplines and the convergence of evolutionary conceptualizations across these (and other) scientific communities provide further sociological evidence of the richness and rigor that 21st century evolution is a robustly interdisciplinary endeavor.

Model scientific communities	**Description**
Prosocial Schools www.prosocialschools.org	Prosocial Schools is a circle within the international Prosocial World community, which has the mission of consciously evolving a world that works for all. Prosocial integrates theoretical perspectives in evolution, cooperation, and contextual behavioral sciences. Focused on cultivating *psychological flexibility* and *core design principles for cooperation* across levels of organization within communities and societies, Prosocial offers a uniquely synthetic framework for evolving cooperation across cultures and contexts.
Diverse Intelligences www.disi.org	The Diverse Intelligences community of practice is a global network of highly interdisciplinary scientists, artists, and storytellers interested in how humans can better *recognize*, *shape*, and *program* the diverse intelligences of our world (and, perhaps, our universe). Looking across human and non-human diversity, understanding cognition at the level of cellular function, and deepening our ethical application of artificial intelligences are all core areas for Diverse Intelligences scholars, who connect throughout the year, especially during the annual Diverse Intelligences Summer Institute.

Cooperation Science Network www.cooperationscience.org	The Cooperation Science Network is an interdisciplinary network of researchers and science communicators looking at the concept of cooperation across any and all contexts. Again, drawing on research across human and non-human diversity, understanding cooperation dynamics within the cellular interactions of multicellular organisms, the Cooperation Science Network, like the above communities, has a strong interest in emergent applications in society and health from this interdisciplinary evolutionary scientific synthesis.
Doughnut Economics Action Lab www.doughnuteconomics.org	The Doughnut Economics Action Lab (DEAL) has emerged from the work of economist Kate Raworth, whose use of the Doughnut Economy metaphor helps communicate the safe operating space for meeting human needs without exceeding planetary capacity. *Doughnut economics* is premised on an interdisciplinary and evolutionary understanding of humans as a cooperative species. DEAL has been working to advance toolkits for cities and schools to engage community science methods for analyzing the social-ecological dimensions of their communities at local and global scales. These tools are being integrated as core resources in the OpenEvo Community Science Lab module.

The primary (though not exclusive) target participants for OpenEvo are international teacher education programs and students. In this context, during our early launch phases, most students enter the platform in the context of collaborative engagement in our *Human Behavior and Sustainable Development* module (https://openevo-learninghub.eva.mpg.de/course/index.php?categoryid=5). This module serves as foundational training in the conceptual and pedagogical aspects of teaching about human behavior, evolution, and sustainability sciences as interdisciplinary themes within general education contexts and is built upon much of the work presented in this thesis. The module is designed for pre-service educators from across subject areas, with many aspects adaptable for motivated upper secondary students, as well as in-service teacher professional development. The module helps participants develop foundational competencies, while challenging them to apply their skills to the evaluation, development, and improvement of a target area of resources within the OpenEvo ecosystem. That is, pre-service educator engagement in this module serves as one engine of innovation and improvement of content on the site. This module also now serves as the on-boarding for internships and student thesis work within our program at the Max Planck Institute for Evolutionary Anthropology, as well as the basic repository for introductory content for engagement with secondary school classrooms.

As participants engage the *Human Behavior and Sustainable Development* module, they will be exposed to, and provided opportunities for further engagement with, other content across the *featured modules* category. This allows us to expose students to the full diversity of potential in this space, while offering them freedom of choice in where they wish to expend their time in evaluation and improvement of current resources.

3.3 Networked improvement of field site modules

Field site modules represent the space for networked co-design of both *content-focused* modules (focused more on teaching for *conceptual understanding*), as well as *context-focused* modules (focused more on engaging students in *community-based cultural evolution*). As previously described in Eirdosh & Hanisch (2021) and Hanisch et al (2020), our Community Science Lab approach seeks to integrate strongly across these domains.

By conceptualizing regions and schools as appropriate scales for the development of a *community-based field site* for *intentional cultural evolution*, the OpenEvo platform creates an invitation for classroom partners to explore the full breadth and depth of educational potential within the interdisciplinary evolution sciences.

Classroom collaborators in the US and Germany have already begun engaging in the co-design of field site modules for their local aims within the context of the Community Science Lab approach, and in collaboration with the relevant OpenEvo *model scientific community* partners. As this model expands, increased opportunities for networked co-design and the spread of effective open educational resources can be intentionally evolved and adapted to diverse classrooms around the world.

3.4 Conclusions

There is no debate that evolution science in the 21st century is robustly interdisciplinary in nature. The still-evolving discourse is centered on *how* we as evolution educators, education researchers, and scientists should conceptualize this interdisciplinarity, and *what* we should do in practical terms to elevate scientifically adequate evolutionary understandings across future generations.

Some in our field may wish to maintain a status quo in which the concept of evolution is exclusively defined by changes in allele frequencies, with all other applications being "mere analogy". Others, represented across this thesis, prefer to think of the concept of evolution as an abstracted description of particular causal relationships, analogically applicable across complex adaptive systems. Prior to this thesis, the full pedagogical implications of this conceptual divide was only being discussed in some corners of higher education, but not significantly in relation to the K-12 general education context. It remains unclear how evolution education as a field will proceed, however, many will agree that there is an urgency in getting this right.

How students around the world come to understand and seek to influence the (biological, cognitive, behavioral, cultural, and computational) diversity in their everyday lives will surely be a central driver of future sustainability outcomes for our planet. Evolutionary thinking, as with systems thinking, represents a conceptually minimalistic framework for leveraging our human cognitive capacities towards a more generalizable understanding of the human condition. The pursuit of such generalized understanding is not some navel-gazing academic pursuit, nor should it be seen to reduce the centrality of our own individuality. Rather, these generalized understandings represent a *common ground* for working together and learning together towards a world that is more workable for all.

A narrowly gene-centered view of evolution education runs the risk of abstracting out too many of the essential causal drivers of human origins and human futures. Understanding evolution as the interdisciplinary science that it is, represents a previously unmapped source domain for global education innovation. This thesis has sought to clarify the specific conceptual implications of this interdisciplinarity, and offer a framework for improving our evolving toolkit for the networked co-design of open education resources in this space.

Teaching about *human origins* is clearly a domain of current mainstream evolution education that benefits from (if not requires) better integration with current conceptualizations in gene-culture co-evolution (see Chapters 2.3 and 2.4). Such an integration itself requires the evolution education community to become more explicit and systematic about the conceptual and pedagogical implications of applying evolutionary concepts beyond genetic change.

Teaching about *intra-organismal evolution* represents a more peripheral but critical space for further innovation beyond what has been suggested in the articles of this thesis (see Chapters 2.2, 2.3, and 2.5). This topic provides an expanded set of diverse case studies for students to learn about and reinforce appropriate conceptual transfer of evolutionary principles. More provocatively, understanding the *self* as an *evolving system* may have broader implications for student conceptual development and psychological flexibility.

The proposition here that may be furthest off the radar of current evolution education discourse would be the development of our *Community Science Lab* model for advancing a community-based cultural evolution approach to evolution education and school improvement initiatives (see Chapters 2.2 and 2.5). If students can become drivers of positive cultural evolution within their schools and communities while simultaneously developing a reflective theoretical basis for their theories of social change, then the educational potential of teaching evolution as an interdisciplinary science is perhaps higher than some in evolution education have previously imagined. Even so, there are contingents in biology education who may suggest that such work falls outside the purview of the biology curriculum (and may or may not be suitable for other disciplines). To make such an argument would be to misunderstand the emphasis placed throughout this work on teaching for *conceptual understanding*. It is precisely the broad interdisciplinary potential of core evolutionary concepts and principles that both support and require educators from across disciplines to think together about how students can navigate their own development of the landscape.

The OpenEvo Learning Hub is just a *basecamp* on the mountain of interdisciplinary evolution education. Generations worth of work remain to be done to map and develop the full breadth and heights of this new landscape. I invite readers to join us on this journey, there is room for climbers from all disciplines and career stages. The only qualifications are a passion for evolution and education and willingness to work together.

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Appendix A:
Summary of key findings from this thesis

1. Evolutionary science in the 21st century is a robustly interdisciplinary endeavor, yet evolution education and evolution education research communities generally do not currently reflect or engage this fact in any systematic or strategic fashion.

2. The conceptual and pedagogical implications for understanding evolution as an interdisciplinary science within the biology education and general education context are expansive and were largely unmapped prior to this work.

   2.1. Narrow conceptualizations of evolution in exclusively gene-centric terms (i.e. defining the concept of evolution solely in terms of changes in allele frequencies) run the risk of abstracting out significant causal processes in evolutionary change.

   2.2. More interdisciplinary perspectives in evolution science focused on the many causes of changes in trait variation and frequency within complex adaptive systems may offer educators and evolution education researchers an expanded toolkit for advancing evolution understanding and acceptance.

   2.3. Grappling with these conceptual and pedagogical implications of teaching evolution as an interdisciplinary science may challenge some conventional wisdom in evolution education research, but largely suggests a more basic need to increase emphasis on a few conceptual aspects at risk of being obscured within exclusively gene-centric conceptualizations.

3. Accepting the conceptual aspects of evolution as an interdisciplinary science opens new opportunities in evolution education in at least three core domains:

   3.1. **Human origins.** An interdisciplinary approach provides a more coherent framework for understanding the complex gene-culture coevolutionary dynamics that likely drove the origin of our species.

   3.2. **Intra-organismal evolution.** An interdisciplinary approach suggests pedagogical opportunities in helping students transfer their conceptual understanding of *variation producing* and *frequency changing* processes across multiple levels of organization in biological and social systems. This includes a deeper understanding of evolutionary processes within organismal development, across the interdependent domains of morphogenesis, organismal behavior, and cognition.

   3.3. **Community-based cultural evolution.** An interdisciplinary approach can challenge students to advance a theoretically informed context for understanding their own intuitive and quasi-scientific theories of cultural stasis or change within the communities that matter to them.

Appendix B:
Summary of thesis outputs

Thanks to our collaborative, interdisciplinary, and participatory approach, my pursuit of this thesis has led to 50 diverse scientific and science communication outputs that, collectively, represent the generative productivity of teaching evolution as an interdisciplinary science.

Peer-reviewed publications

Hanisch, S., & Eirdosh, D. (2020). Causal mapping as a teaching tool for reflecting on causation in human evolution. Science & Education, 1-30. http://dx.doi.org/10.1007/s11191-020-00157-z

Hanisch, S., & Eirdosh, D. (2020). Educational potential of teaching evolution as an interdisciplinary science. Evolution: Education and Outreach, 13(1), 1-26. http://dx.doi.org/10.1186/s12052-020-00138-4

Hanisch, S., & Eirdosh, D. (2021). Are Humans a Cooperative Species? Challenges & Opportunities for Teaching the Evolution of Human Prosociality. The American Biology Teacher, 83(6), 356-361. http://dx.doi.org/10.1525/abt.2021.83.6.356

Book chapters

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Eirdosh, D., & Hanisch, S. (in press). Teaching interdisciplinary evolution science for sustainable development. In Dajani, R. (in press) The Contemplating Frog.

Book review

Eirdosh, D., & Hanisch, S. (2020). Can the science of Prosocial be a part of evolution education?. Evolution: Education and Outreach, 13. http://dx.doi.org/10.1186/s12052-020-00119-7

Invited commentary

Eirdosh. D., & Hanisch, S. (in press) The Music & Social Bonding Hypothesis DOES require group selection. Commentary in: Savage, P., Loui, P., Tarr, B., Schachner, A., Glowacki, L., Mithen, S., & Fitch, W. (2020). Music as a coevolved system for social bonding. Behavioral and Brain Sciences, 1-36. doi:10.1017/S0140525X20000333

Conference posters and proceedings

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Eirdosh, D.; Hanisch, S.; Zabel, J. (2018) The Nature of Us and Them: Teaching and Learning about the Behavioral Ecology of Ethnocentrism. Poster presented at the Spring School of FdDB, University of Cologne.

Eirdosh, D., & Hanisch, S. (2020). A Community Science Lab for Teaching and Learning about Evolutionary Anthropology. Poster presented at the scientific advisory board meeting of the Max Planck Institute for Evolutionary Anthropology, January 2020, Leipzig, Germany

Eirdosh, D., & Hanisch, S. (2020). Community Science Approaches to Understanding the Evolution of Everyday Cooperation. Poster presented at the conference of the European Human Behavior and Evolution Association (EHBEA), March 2021, Virtual Conference. http://dx.doi.org/10.13140/RG.2.2.28393.62562

Eirdosh, D. & Hanisch S. (2021). Evolving an open, networked, and interdisciplinary evolution education research community. Presented at the Cultural Evolution Society, Virtual Conference 2021, Sapporo, Japan

Eirdosh, D. (in press). Diverse Intelligences on OpenEvo: Evolving Concepts and Community in the Classroom. Proceedings of the Diverse Intelligence Summer Institute.

Youth review

*Cronin K.A., & Hopper L.M. (2020). Do Monkeys Care What Is Fair? Front.Young Minds 8:550299. https://kids.frontiersin.org/articles/10.3389/frym.2020.550299

*Youth review process facilitated by Dustin Eirdosh as part of the Community Science Lab at the Max Planck Institute for Evolutionary Anthropology

Young minds article format

Hanisch, S., Eirdosh, D., Schaefer, M., & Haun, D. B. M. (2021). What is “fair” is not the same everywhere. Frontiers for Young Minds, 9: 580435. https://kids.frontiersin.org/articles/10.3389/frym.2021.580435

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Websites

- http://www.GlobalESD.org
- http://www.EvoKids.org

- http://openevo.eva.mpg.de
  - http://openevo-learninghub.eva.mpg.de
  - http://music.eva.mpg.de

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Eirdosh, D. (2020). Why human behavior is at the center of education. TEDxLeipzigInternationalSchool. https://youtu.be/yxaTavNCD74

Eirdosh, D. (2021). Diverse Intelligences on OpenEvo. OpenEvo. https://youtu.be/Eeqmc_M10jU

Eirdosh, D., & Hanisch, S. (2021). Schools as Field Sites - Researcher Introduction. OpenEvo. https://youtu.be/Lra7nUecwvc. Supplementary video to Eirdosh, D. & Hanisch S. (2021) Evolving an open, networked, and interdisciplinary evolution education research community. Presented at the Cultural Evolution Society, Virtual Conference 2021, Sapporo, Japan

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Hanisch, S., Eirdosh, D., & Atkins, P.W.B. (2020). Community Science Field Guide for School Culture: Tools for learning better, together. GlobalESD. http://CommunityScience.GlobalESD.org

Hanisch, S., Eirdosh, D., & Atkins, P.W.B. (2020). Community Science Field Guide for School Gardens: Tools for understanding and fostering cooperation in school garden groups. GlobalESD. http://CommunityScience.GlobalESD.org

Popular press / science communications

Evolution: This View of Life.

Eirdosh. D., & Hanisch, S. (2020). Evolution Education Without Borders: A Collection of Essays on Teaching Evolution as an Interdisciplinary Science. Evolution: This View of Life. https://thisviewoflife.com/evolution-education-without-borders-a-collection-of-essays-on-teaching-evolution-as-an-interdisciplinary-science/

> Eirdosh. D., & Hanisch, S. (2020). Education is an Evolutionary Science. Why Don't We Teach It That Way?. Essay In Eirdosh. D., & Hanisch, S. (2020). Evolution Education Without Borders: A Collection of Essays on Teaching Evolution as an Interdisciplinary Science. Evolution: This View of Life. https://thisviewoflife.com/education-is-an-evolutionary-science-why-dont-we-teach-it-that-way/
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Eirdosh, D., & Hanisch, S. (2021). Black boxing "the environment": the last bastion of faith-based evolution education? NPJ Science of Learning Community. https://go.nature.com/37KaqgZ

Eirdosh, D., & Hanisch, S. (2021). Niche construction: an underutilized concept for evolution education. NPJ Science of Learning Community. https://go.nature.com/3pY9yfM

Hanisch S., & Eirdosh, D. (2021). What Is “Fair” Is Not the Same Everywhere. NPJ Science of Learning Community. https://go.nature.com/2RU8w8P

Appendix C:
Form 2: Publication information

<u>FORMULAR 2</u>

Manuskript Nr. 1

Kurzreferenz Hanisch & Eirdosh (2021), American Biology Teacher

Beitrag des Doktoranden / der Doktorandin

Beitrag des Doktoranden / der Doktorandin zu Abbildungen, die experimentelle Daten wiedergeben (nur für Originalartikel):

Hinweis: Die Manuskripte enthalten keine relevanten Abbildungen (d.h. keine Abbildungen, die experimentelle Daten wiedergeben)

<u>FORMULAR 2</u>

Manuskript Nr. 2

Kurzreferenz Eirdosh & Hanisch (2021), Evolution: Education and Outreach

Beitrag des Doktoranden / der Doktorandin

Beitrag des Doktoranden / der Doktorandin zu Abbildungen, die experimentelle Daten wiedergeben (nur für Originalartikel):

Hinweis: Die Manuskripte enthalten keine relevanten Abbildungen (d.h. keine Abbildungen, die experimentelle Daten wiedergeben)

FORMULAR 2

Manuskript Nr. 3

Kurzreferenz Hanisch & Eirdosh (2020), Evolution: Education and Outreach

Beitrag des Doktoranden / der Doktorandin

Beitrag des Doktoranden / der Doktorandin zu Abbildungen, die experimentelle Daten wiedergeben (nur für Originalartikel):

Hinweis: Die Manuskripte enthalten keine relevanten Abbildungen (d.h. keine Abbildungen, die experimentelle Daten wiedergeben)

FORMULAR 2

Manuskript Nr. 4

Kurzreferenz Hanisch & Eirdosh (2020),Science & Education

Beitrag des Doktoranden / der Doktorandin

Beitrag des Doktoranden / der Doktorandin zu Abbildungen, die experimentelle Daten wiedergeben (nur für Originalartikel):

Hinweis: Die Manuskripte enthalten keine relevanten Abbildungen (d.h. keine Abbildungen, die experimentelle Daten wiedergeben)

<u>FORMULAR 2</u>

Manuskript Nr. 5

Kurzreferenz Eirdosh & Hanisch (2021), COVID-19: Paving the Way for a More Sustainable World

Beitrag des Doktoranden / der Doktorandin

Beitrag des Doktoranden / der Doktorandin zu Abbildungen, die experimentelle Daten wiedergeben (nur für Originalartikel):

Hinweis: Die Manuskripte enthalten keine relevanten Abbildungen (d.h. keine Abbildungen, die experimentelle Daten wiedergeben)

Appendix E: Declaration of honor

Declaration based on Section 5 of University of Jena PhD Regulations

I, Dustin Eirdosh, confirm the following in relation to my request for opening the Doctoral examination process within the University of Jena:

- ❖ I produced the doctoral thesis project myself (see statement of authorship, Appendix C).
- ❖ I neither used any text passages from third parties nor my own final theses without citing those.
- ❖ I have cited the tools, personal information, and sources that have been used.
- ❖ I have provided the names of the persons who assisted me in selecting and analyzing materials, and supported writing of the articles within the thesis (see statement of authorship, Appendix C).
- ❖ I did not receive any assistance from specialized consultants and that any third party did not receive either direct or indirect financial benefits from me for the work connected to the doctoral thesis submitted.
- ❖ I have not already submitted the doctoral thesis project as a final thesis for a state examination or other scientific examination.
- ❖ I did not submit the same, substantially similar, or another scientific paper to any other institution of higher education or to any other faculty.

Dustin Eirdosh, September 21st, 2021

Appendix E: Curriculum vitae

Dustin Eirdosh, M.Sc.

dustin.eirdosh@eva.mpg.de

Date of birth: April 25th, 1982

Research Profile

I am interested in how advances in evolutionary theory relate to current classroom practices in evolution education. Specifically, I am exploring how conceptual relationships across human evolution, behavior, and sustainability sciences can contribute to innovations in interdisciplinary teaching across K-12 education.

- Evolution education
- Teaching for transfer of learning
- School culture
- Social-Emotional Learning
- Interdisciplinary education
- School improvement

Relevant professional experience

April 2019 - Present
Education development coordinator
Department of Comparative Cultural Psychology
Max Planck Institute for Evolutionary Anthropology

August 2018 - present
Co-Founder and Curriculum Designer
Project EvoLeipzig (www.evoleipzig.de)
in collaboration with the Leipzig Zoo school, AncientAncestors.org, and the Max Planck Institute for Evolutionary Anthropology

March 2017 - Present
Doctoral candidate
Leipzig Research Center for Early Child Development
Thesis: Are humans a cooperative species: everyday conceptions and scientific clarification for sustainability science education

March 2017-April 2019
Research assistant
University of Leipzig, Faculty of Life Sciences, Biology Education Research Group

June 2015 - Present
Co-Founder and Curriculum Designer
Global ESD (www.GlobalESD.org)

September 2012 - June 2015
Project leader & curriculum consultant
The Positive Education Action-Research Lab
Toliara, Atsimo Andrefana, Madagascar
University of Toliara, Madagascar (ENS - Faculty of Educational Psychology)

September 2004 - March 2009
K-12 Service-Learning & Youth Advocacy Coordinator
Mt. Desert Island Regional School Unit, Coordinated School Health Program
Hancock County, Maine, USA

Relevant education

2015 - M.Sc. International Food Business & Consumer Science, University of Kassel/ Witzenhausen, Germany. Focus on Education for Sustainable Development (ESD)

2004 - B.A Human Ecology, College of the Atlantic, Bar Harbor, Maine
Focus on sustainability education and community development

Scientific Society Memberships

- Cultural Evolution Society (2017-Present)
- Association for Contextual Behavioral Science (2013-Present)