ARTICLE

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

Susan Hanisch[1] · Dustin Eirdosh[1]

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

✉ Susan Hanisch
    susan.hanisch@eva.mpg.de

    Dustin Eirdosh
    dustin.eirdosh@eva.mpg.de

[1] Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

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.
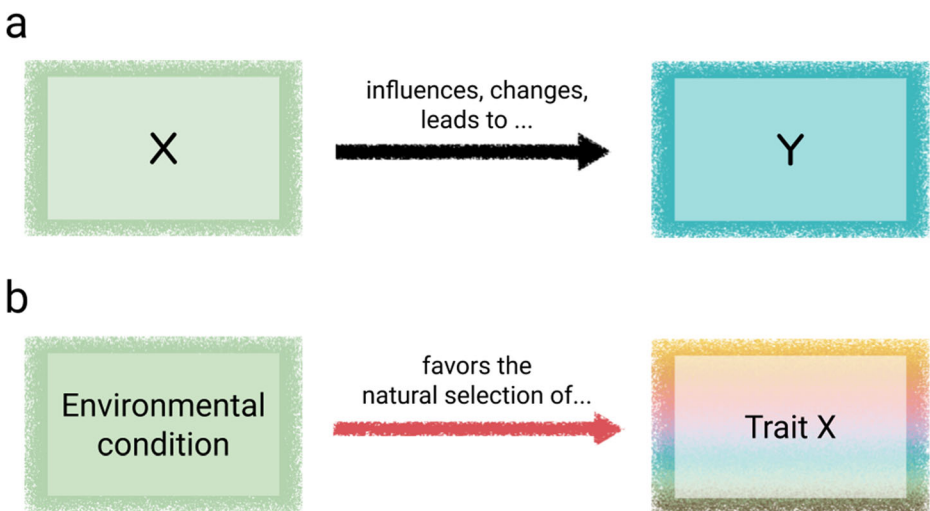

Fig. 1 Key elements of causal maps—nodes and arrows (**a**). An example of a specific causal relationship operating in the natural selection of traits (**b**)
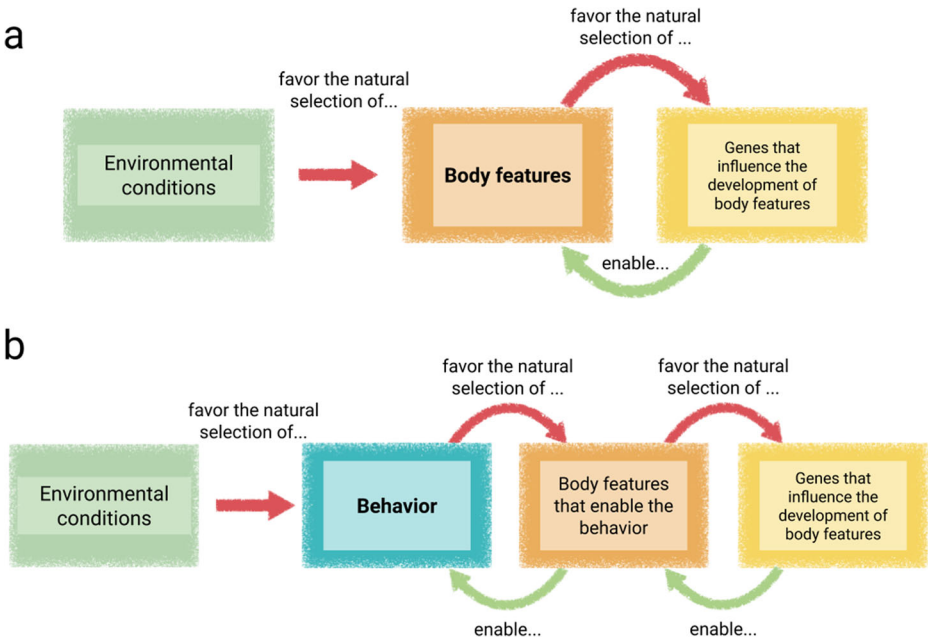
Fig. 2 Hypothetical examples of causal maps in which behavior may not have an important mediating role (**a**) and in which behavior has an important mediating role (**b**) in the evolution and development of a trait complex

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
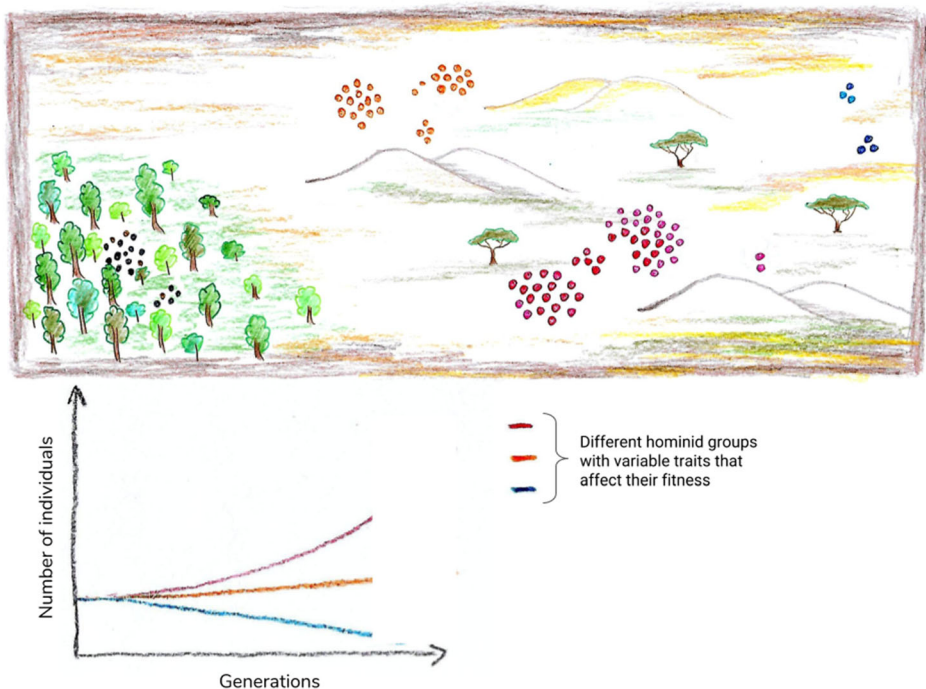

Fig. 3 Schematic drawings and population change graphs which can be reconstructed on classroom chalkboards while engaging students in discussion about *variation* in *populations* and *selection* processes acting on this variation

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).
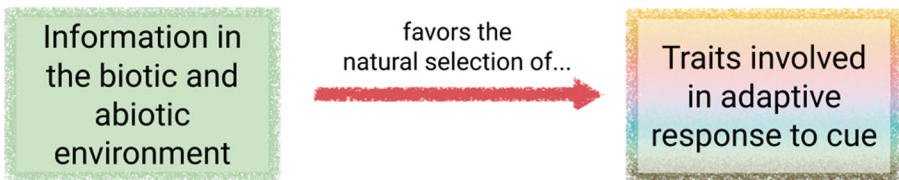
Fig. 4 Example of how causal maps can help differentiate between the instances in which natural selection is a causal mechanism for the existence of a factor or trait, and instances in which it is not, using the example of the difference between "cue" and "signal". **a** An abiotic (such as seasonal 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.
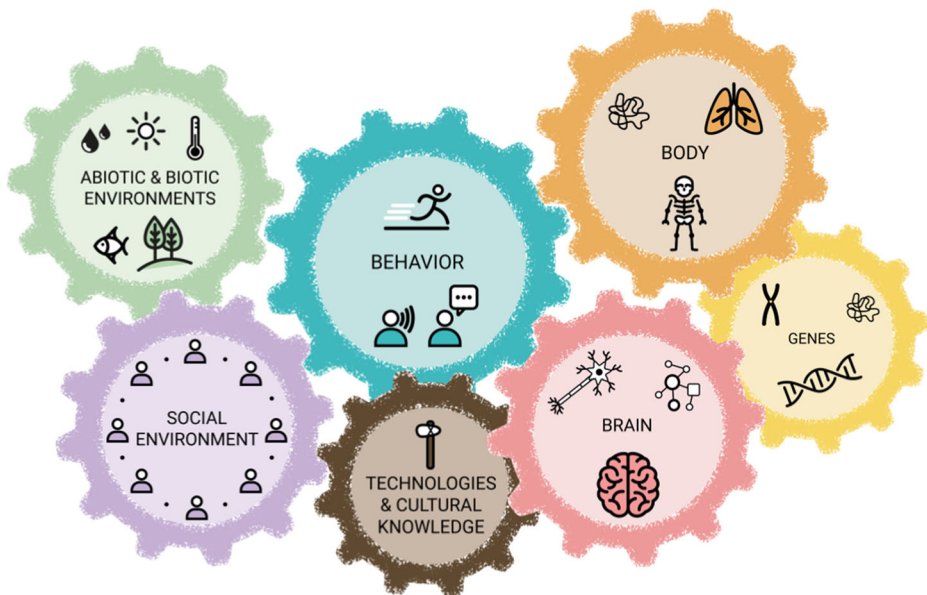

Fig. 5 *Causal domains* of abiotic and biotic environment, social environment, technologies and cultural knowledge (especially in the case of human evolution), behaviors (including cognition), body features, brains, and genes help sort the different causes possibly involved in the evolution and development 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
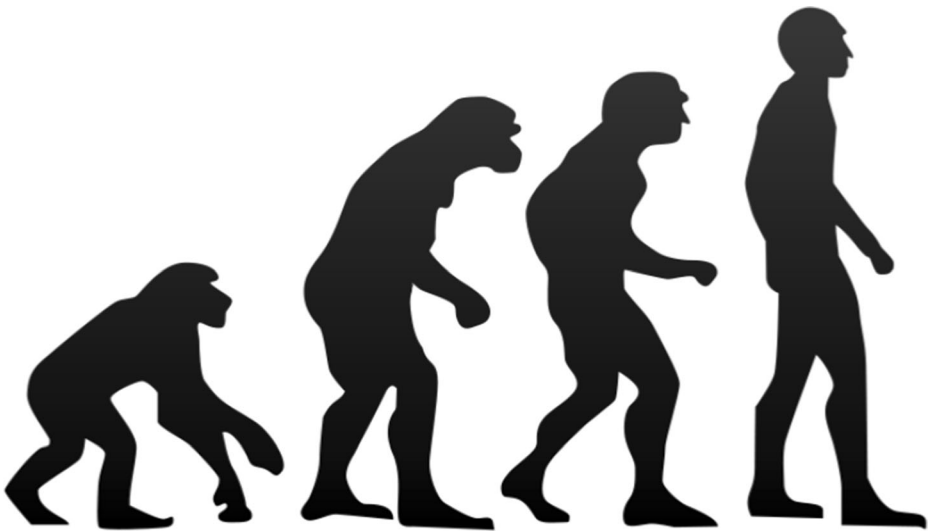

Fig. 6 "March of progress," an icon of evolution often associated with teleological, intentional, or progression-based conceptions of human evolution. Image source: Tkgd2007 (2008); CC-BY-SA 3.0) https://creativecommons.org/licenses/by-3.0/deed.en. https://commons.wikimedia.org/wiki/File:Human_evolution.svg

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
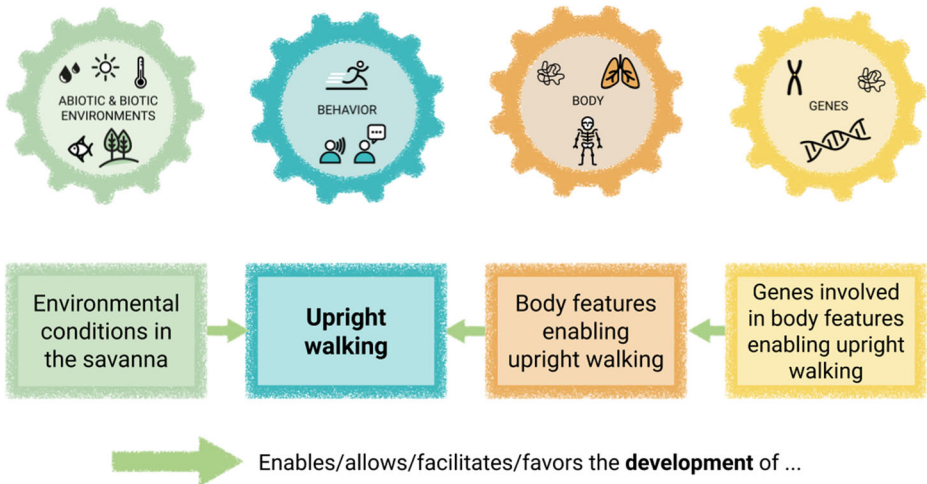

Fig. 8 Causal map of a population of chimpanzees walking upright under certain environmental conditions that elicit this behavior. (1) Environmental conditions may provide more or less strong stimuli for the behavior to be expressed in the population. Assuming that bipedalism does not (yet) have strong 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
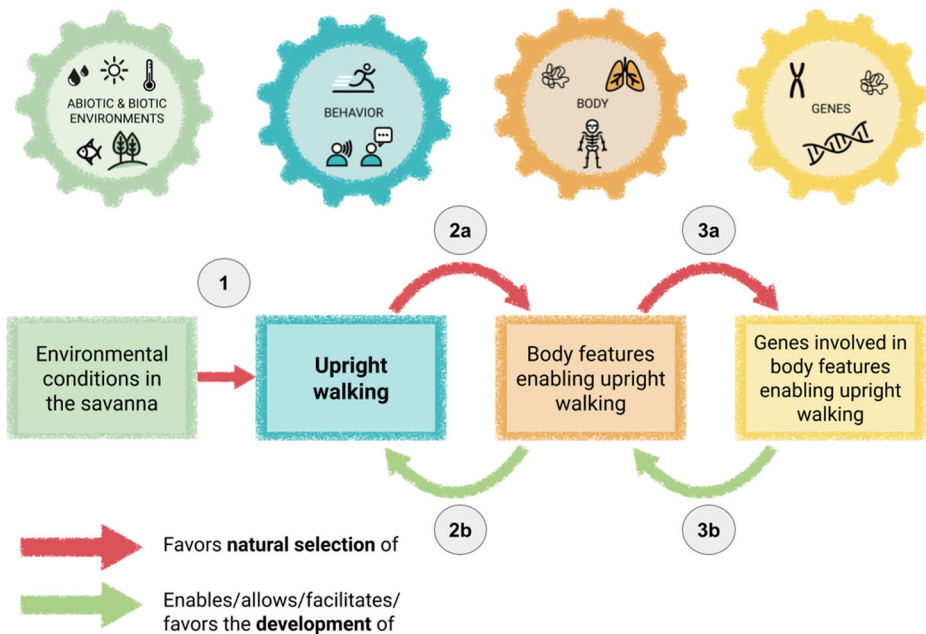

Fig. 9 Causal map of the evolution of upright walking in our hominid line through the interaction of environmental conditions, behaviors, bodies, and genes. (1) Environmental conditions provide a selective advantage to the behavior of upright walking. The behavior would become more frequent in the population. (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
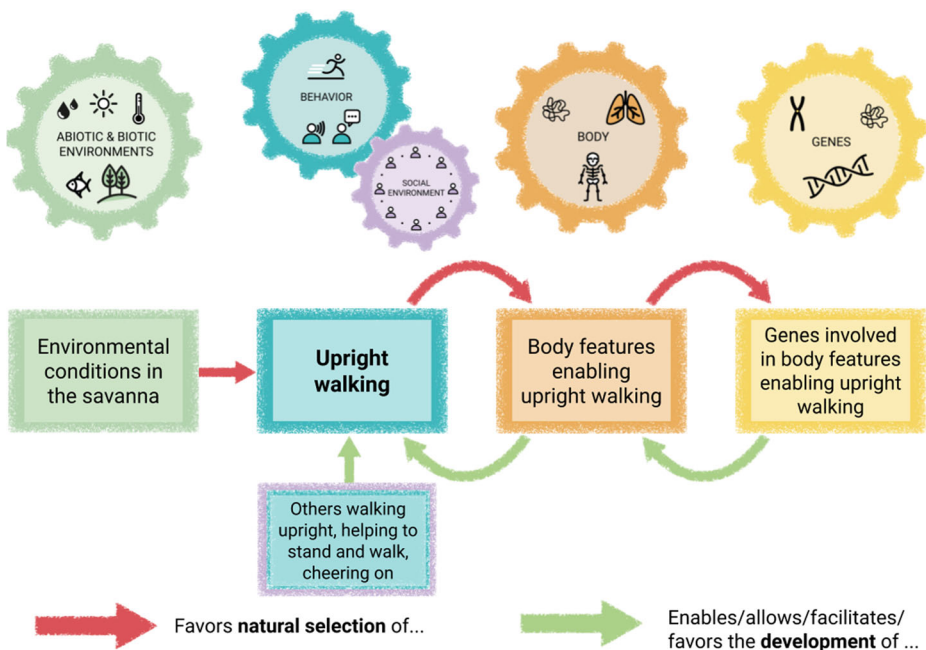

Fig. 11 Causal map of the evolution and development of the phenotype of upright walking with the additional causal role of social environment

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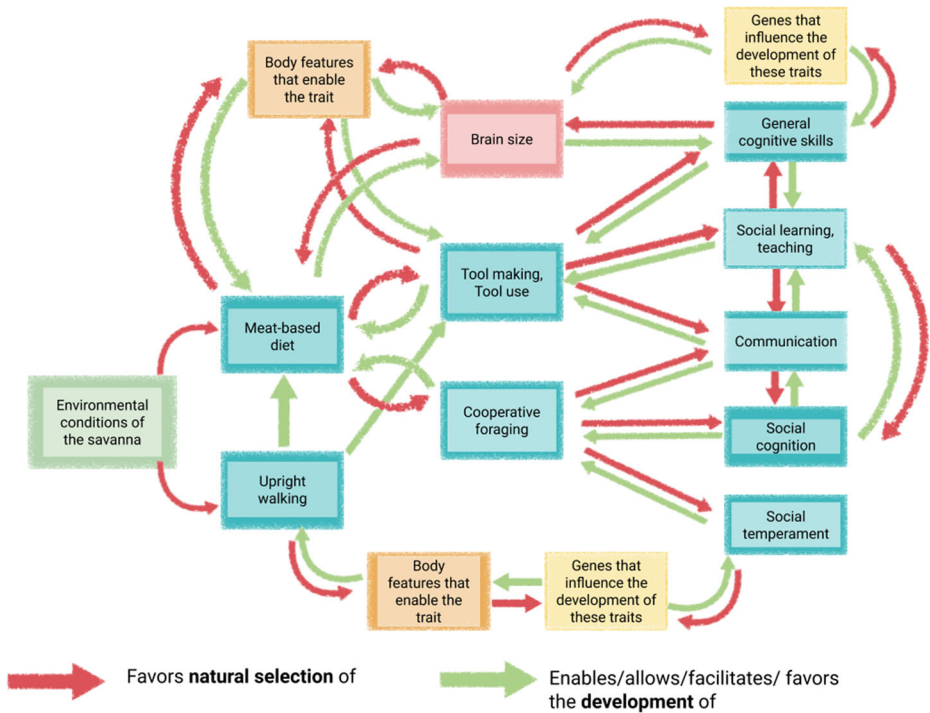
Fig. 12 Causal map showing some of the possible causal linkages that lead to the natural selection and development of various traits during the evolution of the *Homo* lineage. Note the feedback loop between meat-based diet, toolmaking, cognition, and brain size

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.

Compliance with Ethical Standards

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

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