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Translating research on evolutionary transitions into the teaching of biological complexity. II. A NGSS-aligned framework for teaching the hierarchy of life

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Abstract

Complexity is inherent in most biological phenomena, yet there is little effort to teach biological complexity per se in the classroom. Levels of organization and hierarchical complexity are familiar features of living systems and taken for granted in most instructional materials including the Next Generation Science Standards (NGSS) of the United States. However, the evolution of the hierarchical organization of life is not being taught because there has been no instructional framework for doing so until now. We seek to address this gap in instruction by translating recent research on evolutionary transitions in individuality (ETI theory) into an integrative, instructional framework for teaching the hierarchy of life that aligns with the three dimensions of the NGSS. ETI theory presents an evolutionary framework for teaching hierarchical complexity using the social principles of cooperation and confict. These principles are intuitive for students because they are analogous to many of the social situations in their lives. By making use of the ETI framework, instructors can explicitly teach the evolution of the hierarchical organization of life, the organizing framework for all of biology.

Keywords Evolutionary transitions in individuality, Biological complexity, Hierarchy of life, Next Generation Science Standards

Introduction

Complexity is inherent in most biological phenomena, yet there are limited resources available to educators to support the teaching of the evolution of biological complexity at the primary, secondary, or postsecondary

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levels of education. The evolution of complexity does not appear in (1) current descriptions of the three dimensions of the Next Generation Science Standards, the science standards for the primary and secondary levels of education in the United States (NGSS; NGSS Lead States [2013](#page-18-0)), (2) the core concepts and core competencies of the Vision and Change guiding framework for postsecondary biology education (AAAS [2011\)](#page-17-0), or (3) in instructional and curriculum frameworks for biology education (Dauer and Dauer [2016;](#page-17-1) Nehm [2019](#page-18-1)). In addition, the evolution of biological complexity is missing from summaries of pedagogical content knowledge made available to evolution educators (Ziadie and Andrews [2018](#page-19-0), [2019\)](#page-19-1). In our view, the feld of evolution education must address

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this demonstrable gap in instruction by developing instructional frameworks that allow educators to explicitly teach the evolution of complexity.

Here, we focus on a major component of biological complexity: the distinct levels of increasing complexity found in the hierarchy of life. Complexity can be defned and measured in multiple ways, including by the number of parts and number of kinds of diferent parts (McShea [1996,](#page-18-2) [2000](#page-18-3)). More relevant to the hierarchy of life is a defnition of complexity centered on hierarchical complexity, which is measured by the degrees of nestedness of the diferent levels of the hierarchical system (Simon [1962](#page-18-4)). According to evolutionary transitions research (Buss [1987;](#page-17-2) Maynard Smith [1988](#page-18-5), [1991](#page-18-6); Michod [1999\)](#page-18-7), the evolutionary scaffold for the hierarchy of life involves a nested series of evolutionary units, termed evolutionary individuals, which evolved through evolutionary transitions in individuality (ETIs). These evolutionary individuals are the following: molecular replicators or genes, genomes in cells, prokaryotic cells, eukaryotic cells, multicellular organisms, and eusocial insect societies (see Fig. [1\)](#page-1-0). Each of these evolutionary transitions in individuality involved the conversion of groups of evolutionary individuals into a new kind of evolutionary individual in a recursive manner that created life's nested hierarchical structure.

During ETIs, the group becomes increasingly integrated, and individuality evolves through small steps involving cycles of cooperation, confict, and confict mediation (Calcott and Sterelny [2011;](#page-17-3) Carmel and Shavit [2020](#page-17-4); Gissis et al. [2018](#page-17-5); Hanschen et al. [2017](#page-17-6)). Although the transition of groups of individuals into a new kind

of individual evolves in small steps in a continuous fashion, the new level ends up signifcantly more complex than the previous level as the new level includes the old interactions but adds new interactions as well (e.g., multicellular organisms are more complex than cells, eukaryotic cells are more complex than prokaryotic cells, etc.). For this reason, ETIs can be used to teach students about how evolution can explain major jumps in complexity such as those that exist as levels in the hierarchy of life.

Michod et al. ([2022](#page-18-8)) argued that the translation of ETI theory into pedagogic content and practices involves three steps following Gagnier and Fisher's ([2020](#page-17-7)) framework for translating scientifc research into the K-12 classroom. The first step is the specification of the new content that must be taught. In the case of ETIs, this means teaching three core concepts: cooperation, evolutionary individuality, and the hierarchy of life (Michod et al. 2022). The second step involves the development of teaching tools to teach this new content. For ETI content, we have introduced fve teaching tools for this purpose: (1) the volvocine algae as a model system for the evolution of the hierarchy of life, (2) analogies between cooperation and the social lives of students, (3) guided classroom discussions on individuality, (4) cooperation games for exploring cycles of cooperation, confict, and confict mediation, and (5) employing 'tree thinking' to construct phylogenetic trees to show specifc traits important in the evolution of the hierarchy of life. These teaching tools are introduced in Michod et al [\(2022\)](#page-18-8) and further developed in Davison et al. ([in revision\)](#page-17-8). The third step requires developing an

Fig. 1 Elements of the hierarchy of life explained by ETI theory (left panel, adapted from Michod et al. [2022\)](#page-18-8) versus levels of organization as commonly introduced in biology textbooks and instructional materials (right panel). ETI theory explicitly addresses six levels in the hierarchy of life: molecular replicators or genes to genomes in cells, prokaryotic cells to eukaryotic cells, single celled organisms to multicellular organisms, and from multicellular organisms to eusocial societies as seen in social insects such as ants and bees. The levels of organization typically introduced in biology textbooks are molecules, cells, tissues, organs, organ systems, and organisms. In addition, levels above the organism are often included in textbooks, such as ecological communities and ecosystems

instructional framework that connects the new content and teaching tools to the specifc educational context, which includes integrating with relevant learning standards and grade-level benchmarks.

In the present paper, we focus on this third step of Gagnier and Fisher's ([2020](#page-17-7)) translation framework by developing an NGSS-aligned instructional framework and curriculum sequence, summarized in Table [5](#page-15-0) and Fig. [2,](#page-2-0) to enable primary and secondary biology educators to develop curriculum and instruction strategies that explicitly teach the evolution of the hierarchy of life within their educational contexts. ETI theory can be translated into diverse educational contexts to teach students about the evolution of the hierarchy of life. As an example, we consider the educational context in the United States at K-12 levels using the internationally benchmarked NGSS. The NGSS is designed to help students develop a cohesive understanding of disciplinary core ideas, cross-cutting concepts, and scientifc practices through active learning experiences. Over 70% of U.S. teachers base their science instruction, curriculum, and assessment strategies on the NGSS or NGSS derivatives (NSTA [2021](#page-18-9)). The NGSS was developed in the United States based on international benchmarking of 10 countries that were deemed advanced in the instruction of science and math (i.e., Canada, Chinese Taipei, England, Finland, Hong Kong, Hungary, Ireland, Japan, Singapore, South Korea) (NGSS [2010](#page-18-10)). Consequently, the NGSS is refective of the international expectations highpreforming nations have set for their students. Therefore, we develop here a NGSS alignment to discuss how using ETI theory to teach the hierarchy of life can be applied in local (U.S.) and global educational contexts.

Why teach the evolution of the hierarchy of life?

In contrast to the topic of complexity, the hierarchy of life is a familiar topic to biology educators as hierarchical organization is a major framework for many instructional materials. However, the existence of the hierarchy of life is taken for granted in these instructional materials. There are two main reasons to teach the origin and evolution of the hierarchy of life. First, the hierarchical organization of life is a common framework for teaching biology; however, there are no resources available for teaching its origin and evolution. A diagram of the hierarchy of life is often present at the beginning of biology texts, which provides the student with a framework for how the living world is organized, as well as a vocabulary to facilitate thinking on biological processes that span diferent levels of organization. Figure [1](#page-1-0) (right) shows an example of such a diagram compared to the evolutionary levels of the hierarchy of life addressed by ETI theory that we have already introduced (left).

The relevance of hierarchical organization to biology has been acknowledged by the National Academies of Science (National Research Council [2009,](#page-18-11) [2012\)](#page-18-12) and the

Fig. 2 Student understanding of ETIs increases over grade levels as a function of the scope and sequence and depth of understanding. Changes in student understanding are presented as a staircase to illustrate the relationships between lower and upper anchors as students progress through the grade levels. The curriculum sequence for ETIs starts from the lowest anchor, focused on the role of groups in biology, and ends at the highest upper anchor, focused on the nested, hierarchical organization of life. This curriculum sequence teaches the evolution of the hierarchy of life in a way that is readily available for instruction, curriculum, and assessment development in the K-12 classroom

American Association for the Advancement of Science (AAAS [2011](#page-17-0)), who have major guiding documents for curriculum development which use the hierarchical levels of organization as a framework for understanding biological complexity. For example, the National Research Council ([2009](#page-18-11)) states:

The great potential of the life sciences to contribute *simultaneously to so many areas of societal need rests on the fact that biology, like physics and chemistry, relies on a small number of organizational principles. The reality of these core commonalities, conserved through evolution – that DNA is the chemical of inheritance, that the cell is the smallest independent unit of life, that cells can be organized into complex, multicellular organisms, that all organisms function within interdependent communities and that photosystems capture the solar radiation to provide energy for all life processes – means that any knowledge gained about one genome, cell, organism, community, or ecosystem is useful in understanding many others [...] Biologists are increasingly able to integrate information across many organisms, from multiple levels of organization, and about entire systems to gain a new integrated understanding that incorporates more and more of the complexity that characterizes biological systems (p.40-41).*

Despite the pervasiveness of hierarchical organization in teaching materials, the origin and evolution of the hierarchy of life itself is not a topic in these materials. Hierarchical structure was not present at the beginning of life; it evolved, and students should understand how it evolved. Moreover, there are no instructional materials to teach the hierarchy of life beyond acknowledgement of its fundamental importance and discussion of relationships among hierarchical levels. This gap has resulted in the need to explicitly teach the hierarchy of life, as strongly advocated for by both biology education researchers (Dauer and Dauer [2016;](#page-17-1) Nehm [2019](#page-18-1)) and practitioners (Friedrichsen et al. [2016](#page-17-9); Ziadie and Andrews [2018](#page-19-0), [2019](#page-19-1)). Nehm [\(2019\)](#page-18-1) explains:

The hierarchical structure of life, and its corresponding biological scales [...] are repeatedly acknowledged as important considerations about biological systems in nearly every textbook and classroom. Although most (if not all) biology education programs draw student attention to the concepts of scale and hierarchy, they rarely explore how scale and hierarchy elucidate and problematize the functioning of biological systems [...] Yet, a review

of the literature reveals that an explicit curriculum for helping students engage in the meaning of this hierarchical arrangement appears lacking (p. 14).

The second reason to teach the origin and evolution of the hierarchy of life is that not teaching it leaves a major gap in student understanding and an opening for nonscientifc approaches to biological complexity (Behe [1996](#page-17-10); Dembski [2002](#page-17-11)). Behe [\(1996](#page-17-10)) refers to the lack of inclusion of evolutionary mechanisms in biology and biochemistry textbooks and instructional materials as evidence that evolutionary biology cannot explain the complexity present in biological systems. Thus, Behe [\(1996\)](#page-17-10) and others support movements such as intelligent design or 'teach the controversy' in biology classrooms. Although the scientifc validity of intelligent design and related movements have been thoroughly addressed and rejected by the scientifc community (see examples in Lynch [2005](#page-18-13); Scott and Branch [2003](#page-18-14); Scott and Matzke [2007](#page-18-15)), it still remains that evolutionary mechanisms are largely absent, or merely alluded to, in discussions of biological complexity. The instructional gap may incorrectly suggest to the student an inability of evolutionary theory to explain the vast complexity in living systems. Explicit teaching of the evolution of hierarchical complexity serves to fill this instructional gap. Therefore, including ETI theory in the biology curriculum supports efforts to resist non-science approaches in biology.

Evolutionary transitions in individuality: overview and core concepts Overview

ETI theory grew out of research into individuality and the evolution of the hierarchy of life begun by Buss ([1987](#page-17-2)) and research into the major evolutionary transitions begun by Maynard Smith ([1988](#page-18-5)). Buss [\(1987\)](#page-17-2) and Maynard Smith ([1988](#page-18-5), [1991\)](#page-18-6) were interested in explaining in Darwinian terms the diferent levels of complexity present in the hierarchy of life (e.g., replicating molecules, simple cells, eukaryotic cells, etc.). Maynard Smith and Szathmáry ([1995](#page-18-16)) further expanded these ideas in their seminal book with an emphasis on transitions between diferent kinds of information systems. Because of their emphasis on information transfer, they expanded the list of "major transitions" to include not just levels in the hierarchy of life but problems like the evolution of the genetic code, human language, and sex. Michod ([1999\)](#page-18-7) developed a mathematical theory which returned the focus to the evolution of diferent kinds of evolutionary individuals and levels of complexity present in the hierarchy of life, the components of which have been recently summarized (Davison and Michod [2023;](#page-17-12) Hanschen et al. [2015](#page-17-13), [2018](#page-17-14);

Michod [2022](#page-18-17); Michod et al. [2022](#page-18-8)) and is the basis for our treatment here.

In this section, we briefy review three core concepts of ETI theory that serve as the foundation for our development of an integrative instructional framework and curriculum sequence. These core concepts are as follows: (1) individuality and ftness, (2) cooperation, confict, and confict mediation, and (3) the hierarchy of life from the ETI perspective. Explicit instruction and curriculum on each of these core concepts serve to provide students with an evolutionary perspective on the hierarchy of life.

Core concept I: individuality and ftness

There are several conceptions of individuality present within the biological literature (reviewed in Santelices [1999](#page-18-18)); however, ETI theory uses a distinctly evolutionary defnition that equates an individual as a unit of selection and adaptation. Units of selection exhibit heritable variation in ftness and are thus subject to Darwinian evolution (Lewontin [1970](#page-18-19); Okasha [2006\)](#page-18-20). During an ETI, ftness must change from being a property of the previous individual to being a property of the group as the group evolves into a new kind of individual. We have referred to this process by which ftness changes levels of organization as the reorganization of ftness from the old to the new level (Michod [2006](#page-18-21); Shelton and Michod [2014](#page-18-22)). The reorganization of fitness involves the transfer of ftness from the individual to the group level through the specialization of the lower-level units in the ftness components of the group.

At the start of an ETI, the unit of selection is the existing individual. For example, during the evolution of multicellularity, the unit of selection starts as the unicellular organism, the single cell. When cells form groups, cycles of cooperation, confict, and confict mediation can occur, fueling the increased integration of the group. If groups become so integrated that heritability of ftness predominates at the level of the group, ftness becomes a property of the group instead of the pre-existing individuals and the group has become a new kind of individual (Michod [1999,](#page-18-7) [2007](#page-18-23)). In the evolution of multicellularity, this occurs when cells specialize in survival (soma cells) or reproduction (germ cells). Division of labor in the basic components of ftness causes cell ftness to decline (were they to leave the group) while ftness of the cell group increases; for instance, cells that are specialized in survival cannot reproduce when alone and therefore the ftness of those specialized cells is reduced. Because ETIs are centered around ftness, and how it is reorganized into groups, teaching ETIs can be tied to curriculum elements that are related to survival and reproduction, natural selection, cellular interaction, system integration, and physiology. Indeed, the concept of "individuality" may be initially presented in the classroom as "that" which both survives and reproduces on its own. "Individuality" can also be presented during those common discussions about what life is that occur at almost all grade levels.

Core concept II: cooperation, confict, and confict mediation

Once groups form, members may interact in multiple ways, including by cooperating. Cooperation occurs when individuals in a group beneft from working together. Cooperation can take multiple forms and involve diferent kinds of benefts, depending on the nature of the cooperating individuals and the interactions involved. If there are costs associated with cooperation, individuals that cheat by benefting from the cooperation of others without cooperating themselves will be favored by selection within the group. Cheaters may destabilize the group by taking advantage of shared resources without contributing to them and potentially reproducing more quickly than cooperators. Such cheating can be inhibited if mechanisms that mediate conflict evolve. These so-called confict mediating mechanisms include the evolution of single cell bottlenecks that align the ftness interests of the individuals that make up the group or of costly punishments for cheaters such as with the immune system of some animals. Cycles of cooperation, confict, confict mediation, and enhanced cooperation can occur during the evolution of new kinds of individuals. Finally, the evolution of division of labor in the basic components of ftness, survival and reproduction, inextricably ties the ftness of group members to the ftness of the group as a whole, as members can no longer survive and reproduce on their own. At this point, what had been considered a group is now a new kind of individual (Michod and Nedelcu [2003;](#page-18-24) Queller [1997](#page-18-25)).

Core concept III: hierarchy of life

Life's hierarchical organization evolved through repeated ETIs, giving rise to the nested hierarchical organization that we see today. These transitions include the transition from molecular replicators or genes to genomes in cells, from multiple prokaryotic cells to eukaryotic cells, from single cells to multicellular individuals, and from multicellular individuals to eusocial societies as seen in social insects. Each of these levels of organization within the hierarchy of life are new kinds of individuals (i.e., units of selection), each of which started out as a group of individuals from the previous level. Therefore, the hierarchy of life itself is seen as a series of increasingly inclusive and nested units of selection as frst identifed by Buss [\(1987\)](#page-17-2) and Maynard Smith ([1988,](#page-18-5) [1991\)](#page-18-6).

ETI theory addresses the evolutionary backbone of the hierarchy of life and not the non-evolutionary levels that also arise both ecologically, such as communities and ecosystems, and within organisms, such as organs and tissues (see Fig. [1](#page-1-0)). Many textbooks having depict the hierarchy of life containing levels of organization that are units of selection (e.g., genomes, cells, organisms) and levels of organization that are not units of selection (e.g., tissues, organs, organ systems, biological communities, ecosystems). ETI theory only considers levels of organization that are units of selection, and thus provides the basic evolutionary scafold which provides a context for functional levels of organization to exist such as those that exist within the multicellular organism: tissues, organs, and organ systems. While these functional levels are not evolutionary individuals, they may be explained using principles of cooperation and confict discussed above (see, for example, Brückner et al. [2021](#page-17-15)). Likewise, most diagrams of the hierarchy of life include higher level assemblies such as communities and ecosystems that are also not evolutionary levels as they are not units of selection (Maynard Smith [1988](#page-18-5)). Although not all levels in the hierarchy of life are evolutionary individuals, evolutionary individuals make up the basic evolutionary scaffold of the hierarchy of life.

ETIs as a unifying framework in teaching biology

ETI theory explains large jumps in hierarchical complexity and the broad scale diversifcation of life using smaller evolutionary steps that follow the Darwinian paradigm of continuous evolution, with each small step being advantageous in and of itself. Since the theoretical framework explaining ETIs is built upon Darwinian principles of continuous evolution and the two components of ftness (survival and reproduction and their reorganization) are central to ETIs, studying these transitions can help students understand natural selection and evolution generally. Moreover, the inclusion of ETIs in the biology curriculum may help students bridge the gap between microevolution and macroevolution, a distinction which is commonplace in teaching evolutionary biology (Nehm and Kampourakis [2014](#page-18-26); Novick et al. [2014\)](#page-18-27) and included in the NGSS. The mechanisms underlying ETIs are standard microevolutionary processes in group-structured populations, however the outcome is perhaps the most macro-level feature of life, its hierarchical organization and complexity.

ETIs can be used to understand and to teach students about how hierarchical complexity evolves and how evolution can explain major jumps in complexity using an intuitively familiar framework. Students are social beings and can intuitively grasp many of the concepts such as cooperation and confict resolution upon which ETIs are based. Using ETIs, students can ask questions regarding the origin and evolution of the hierarchy of life in a manner that integrates other key ideas in the biological sciences, including biological diversity, cell biology, heredity, and the ftness-based components of survival and reproduction. Moreover, ETI theory provides an evolutionary mechanism for understanding the evolution of the hierarchy of life that can be problematized into empirically testable hypotheses and predictions, and therefore provides the student and teacher with an integrated teaching framework. As such, this work aims to contribute to the pedagogical content knowledge available for evolution educators (Ziadie and Andrews [2018](#page-19-0), [2019\)](#page-19-1) and to complement pre-existing instruction and curriculum strategies in evolution education by contributing a framework for teaching the evolution of the hierarchy of life.

An integrative instructional framework and curriculum sequence for the evolution of the hierarchy of life

Overview

As a frst measure of demonstrating how ETI principles can provide an integrative instructional framework for learning the origin and evolution of the hierarchy of life, we operationalize our framework by developing a scafolded curriculum sequence with key learning outcomes. This curriculum sequence is a direct result of the translation of the core ETI concepts to allow students to understand the key evolutionary mechanisms leading to the evolution of hierarchical complexity. To support student understanding of the evolution of the hierarchy of life through the study of ETIs, we present each of the core content areas of ETI theory as levels of understanding for the curriculum sequence. Each of these levels of understanding are anchored in two diferent places: the "lower anchor," which characterizes students' incoming set of knowledge about a topic, and the "upper anchor," which defnes the target level of sophistication of knowledge as established by the instructor and/or the scientifc community (National Research Council [2007](#page-18-28); Scott et al. [2019\)](#page-18-29). Each of these levels of the curriculum sequence are iterative in that the upper anchor for one level is the lower anchor for the next level. This scaffolded approach to the curriculum sequence allows students to develop their understanding of ETI theory in a progressive manner that builds more sophisticated, scientific understandings with each succeeding level. This scaffolded sequence is as follows:

- (1) *Level I: Groups* Students begin with the concept that groups of individuals can do things that single individuals cannot and that individuals can beneft from cooperating in groups.
- (2) *Level II: Cooperation* Students will learn that cooperating in a group helps individuals with tasks related to survival and reproduction such as obtaining food, defending themselves, and coping with environmental changes. However, cooperation creates an opportunity for cheating which can decrease the survival of cooperating group members.
- (3) *Level III: Individuality* Students will focus on the concept of the evolutionary individual. Students learn there are diferent kinds of individuals that survive and reproduce and that individuals can form groups in which they cooperate by specializing in collective goals such as group survival and reproduction.
- (4) *Level IV: Hierarchy of Life* Students will apply their understanding of cooperation, division of labor, and evolutionary individuality to understand that the nested, hierarchical organization of life is due to the repeated evolution of diferent kinds of cooperating groups into diferent kinds of individuals.

Within these discrete levels, we present multiple key learning outcomes that guide the curriculum sequence in each level. These key learning outcomes allow students to navigate intermediate steps and serve as signposts for the development of curriculum and instruction that will guide students towards the upper anchors.

As a proof of concept of the relevance of our framework and curriculum sequence to the local educational context, as well as further explanation of how ETI theory can directly address core biological ideas currently present in curriculum and instruction in the life sciences, we align the general principles of ETI research onto the three dimensions of the NGSS. These dimensions are: (1) *science and engineering practices*, the specifc set of skills necessary for participation in the scientifc and engineering process, (2) *crosscutting concepts*, concepts that have applications across all disciplines in the sciences, and (3) *disciplinary core ideas*, which are specifc scientifc core concepts relevant to the life sciences. The NGSS itself serves to operationalize the vision described by the National Research Council's *A framework for K-12 science education* (National Research Council [2012\)](#page-18-12), by synthesizing each of the dimensions into three-dimensional performance expectations that can be readily used by classroom teachers to guide instruction, curriculum, and assessment. A further explanation of the NGSS, its performance expectations,

and a guide for their implementation into the classroom, can be found in Krajcik et al. [\(2014\)](#page-18-30). For the purposes of the present paper, we focus only on NGSS performance expectations, however we provide an in-depth alignment of the general principles of ETI theory to the three dimensions of the NGSS in Supplementary Materials [S2.](#page-17-16)

Each of these key learning outcomes are aligned with specifc sample NGSS performance expectations to show that ETI theory is related to a pre-existing concept in the NGSS. Our alignment of these key learning outcomes to NGSS performance expectations refect a vertical coherence in the curriculum across NGSS grade bands to support learning about ETI theory. Therefore, we have designated each level of the curriculum sequence to follow the progression of NGSS grade bands (e.g., level 1 of the curriculum sequence is aligned with the NGSS K-2 grade band, level 2 is aligned with the NGSS 3–5 grade band, etc.). However, this is not an implied restriction that our sequence must be used as described here; our developed curriculum sequence can be used at any grade level.

Level I: Groups

Our curriculum sequence begins with the role groups play in biology (the frst step in an ETI). Even at an early age of 5 or 6 years-old (but as early as 3.5 years old; Olson and Spelke [2008](#page-18-31)), students have an intuitive understanding of groups and group membership based on the concept of cooperation (Plötner et al. [2016](#page-18-32)); that is, children can distinguish between collections of individuals that constitute a group versus collections of individuals that are not groups. These results suggest that students' understanding of groups and behavioral expectations of cooperation and mutual aid are an appropriate lower anchor for this level. The lower anchor is as follows: *Groups are collections of individuals that exhibit cooperative and/or collaborative behavior, such as sharing, that can result in preferential distribution of resources to group members.*

Starting from this lower anchor, we describe (1) the upper anchor for this level of the curriculum sequence, (2) key learning outcomes to help students obtain the upper anchor, (3) alignment of each of these key learning outcomes to sample pre-existing NGSS performance expectations for the NGSS K-2 grade band, and (4) key insights about ETI theory that are necessary to understand to achieve the upper anchor. The first level of the curriculum sequence is summarized in Table [1](#page-7-0).

We describe the basic structure of Table [1](#page-7-0) in detail since this structure will be used for the other levels below (Tables $2, 3, 4$ $2, 3, 4$ $2, 3, 4$ $2, 3, 4$). The first row represents the lower anchor, and the last row represents the upper anchor

Table 2 Summary of alignment of the key learning outcomes of cooperation in ETI theory to sample NGSS performance expectations along with key insights
Lower Anchor: Groups of individuals can do things that single individ

for the level. The left column contains each of the key learning outcomes to aid students in progressing from the lower anchor towards the upper anchor, and therefore represents the necessary concepts students need to learn to successfully reach the upper anchor. The middle column lays out the alignment of each key learning outcome to pre-existing NGSS performance expectations. The right column presents key insights about ETI theory that are added benefts of including ETI-related concepts in the curriculum. This pattern will be maintained for each of the levels in the curriculum sequence.

From students' intuitive understanding of groups and group members, as represented in the lower anchor, students can be introduced to examples of groups in nature, such as ants in a colony or bees in a beehive, and how these groups must work together to complete tasks related to their survival. This would allow students to think about how individuals accomplish tasks while working with others. It would also serve as a platform to think about groups and cooperation within biological scenarios related to survival and reproduction. The introduction of the role of groups in biology, and how groups can aid in the survival of members, enables future discussions on cooperation, individuality, and the hierarchy of life. As a result, a task-oriented teaching context would allow students to reach our upper anchor for the K-2 grade band, which is the following: *Groups of individuals can do things that single individuals cannot. Individuals can beneft from cooperating in groups.*

The first and third key learning outcomes, located in the frst and third rows of Table [1,](#page-7-0) respectively, focus on the intrinsic cooperative property of groups as applied to biological scenarios as well as how group living can affect the survival of both parents and offspring. The second key learning outcome, located in the second row of Table [1](#page-7-0), applies the concept of groups to the social dimensions of habitats. When the concept of habitat is presented in the classroom, there are discussions on the abiotic and biotic factors infuencing the environment, or habitat by which group interactions can occur. It should be recognized that biotic factors also include the social environment. The social environment affects behavioral diversity within groups of individuals, including what behavioral activities, or tasks, individuals can accomplish alone and with others. This behavioral diversity should be included with students' general constructs of biodiversity.

Level II: Cooperation

The study of cooperation builds off an intuitive understanding of the importance of group dynamics in accomplishing larger, complicated tasks are done easier when more than one individual is involved. This intuitive

understanding corresponds with child development, as discussed in the previous level, and with the realization that students encounter tasks in everyday life. These relatable, applicable ideas allow us to present the lower anchor of our learning progression for understanding the role of cooperation in biology: *Groups of individuals can do things that single individuals cannot. Individuals can beneft from cooperating in groups.*

In our efforts to support the learning of the evolution of hierarchical complexity via the study of ETIs and individuality, we continue our studies with the content area of cooperation due to this concept being most intuitive and accessible for students' naïve conceptualizations of biology. Students learn about cooperation, how it afects survival, and how cooperation in groups can lead to cheating. They also learn about the survival consequences of widespread cheating in groups. Students can conceptualize instances of cooperation and cheating in nature by studying individuals they may be more familiar with, such as charismatic megafauna and domestic animals. Examples of how cooperation in nature afects survival provide an alternative to the traditional 'red in tooth and claw' view of survival.

Making cooperation an integrative part of biological interactions lays a foundation for an understanding of how hierarchical complexity can evolve through evolutionary mechanisms. This foundation serves as an intermediate step for understanding ETIs in individuality since cycles of cooperation and confict are the primary mechanisms by which these transitions occur (Michod [2007](#page-18-23)). Next is an explicit discussion on individuality, which serves as a content area of ETI theory and builds upon student understanding of cooperation. To achieve preparation for discussions of individuality, we have identifed the following upper anchor, which is a modifcation of the original grade end point for grades 3–5 for disciplinary core idea LS2.D (National Research Council [2013](#page-18-33)): *Cooperating in a group helps individuals with activities related to survival and reproduction, such as obtaining food, defending themselves, and coping with changes*. *However, cooperation creates an opportunity for cheating which can decrease the survival of cooperating group members.*

The first and second key learning outcomes provide. two foundational concepts: (1) the defnition of cooperation, and (2) individuals vary in the ways they interact, as both cooperation and cheating can occur in groups. Variation among individuals afects the ability by which individuals can obtain food, defend themselves, and cope with environmental changes and stressors. Members of cooperative groups may possess an increased level of ftness due to their collective

ability to complete tasks. If numerous individuals in a group are cheating by benefting from the cooperators' behavior while not contributing to the group, the group will be less likely to persist. Therefore, cooperation and cheating among individuals in a group can have a direct infuence on survival, which is the focus of the third key learning outcome. The fulfillment of each of these key learning outcomes for this level allows students to possess a deeper understanding of how cooperation is related to survival. Students master this level with the understanding that cooperation can help individuals survive but that cheating must be controlled if the group is to persist. The upper anchor, lower anchor, key learning outcomes, sample alignment to NGSS performance expectations, and key conceptual insights for this level of the curriculum sequence are summarized in Table [2](#page-8-0).

Level III: Individuality

Individuality, in addition to cooperation, serves as the foundation for ETI theory's explanatory power of the hierarchical organization of life. At this stage in the curriculum sequence, students should understand the role that cooperation itself plays in biology. Students should also understand that cooperation and cheating afect the likelihood of survival, a key part of the 'upper anchor' for the cooperation content area. As such, the upper anchor of the previous section will serve as the lower anchor for this section: *Cooperating in a group helps individuals with activities related to survival and reproduction, such as obtaining food, defending themselves, and coping with changes. However, cooperation creates an opportunity for cheating which must be mediated if the group is to survive.*

At the start of the curriculum sequence, students may understand the term 'individual' as one solitary individual (e.g., a bear) or a part of an individual (e.g., a flower). In the ETI framework individuals are units of selection and adaptation that both survive and reproduce. At this level, students focus on learning what an evolutionary individual is, that there are diferent types of individuals that may form social groups, and that cooperation among individuals afects survival and reproduction of both the individual and the group. This is represented in the upper anchor for this section: *There are different kinds of biological individuals such as unicellular, multicellular, and social insect colonies. Individuals can form groups in which they cooperate by specializing in collective goals such as group survival and reproduction.*

The first key learning outcome is an understanding of the defnition of an evolutionary individual as entities that can survive and reproduce on their own and are subject to evolutionary processes. This represents the transition of students from a naïve conceptualization of an individual as an organism to one that centers survival and reproduction and therefore begin to place individuality within an evolutionary context. Once students understand the defnition of an evolutionary individual, they learn about diferent types of evolutionary individuals for the second key learning outcome. Students are presented with diferent examples—especially those that are most pertinent to the evolution of multicellularity and the evolution of hierarchical complexity. Students learn that unicellular organisms and multicellular organisms are diferent kinds of evolutionary individuals, and that the eukaryotic cell is a diferent kind of individual from bacterial and archaeal cells.

Once students have a foundational understanding of the defnition of evolutionary individuals, as well as the application of the concept of groups to cells (both eukaryotic and prokaryotic), they can study the third key learning outcome. The third learning outcome focuses on division of labor among members of a group. Students will have learned that diferent types of individuals that may form social cooperative groups. The study of division of labor among cooperating members of a group allows students to understand how the ftness of each individual is linked to other group members in the context of the group. By focusing on group relationships and dynamics, students can begin to shift their thinking from only considering the ftness of individuals to considering the ftness of the entire group. Further, they can apply this understanding to examine cooperative interactions, including division of labor, among the parts of a cell and among the cells that make up a multicellular organism. Integration of these concepts will not only complement the pre-existing curriculum of cell theory, genetics, and evolution, but extends and applies these core concepts to answering questions related to the evolution of hierarchical complexity. These concepts build off the cooperation module and set students up to understand the hierarchy of life itself. The key ideas of this level of the curriculum sequence are summarized in Table [3.](#page-9-0)

Level IV: Hierarchy of life

The final stage of the curriculum sequence for ETI theory focuses on placing the general principles of social and group dynamics, cooperation, and individuality within an evolutionary context to allow students to directly address the question of how life's hierarchical organization could have evolved. These core concepts of ETI theory coalesce, integrating with other biology concepts regarding cellular processes, Mendelian inheritance, variation in traits, and evolutionary processes, to provide students with an integrated framework for asking questions about the evolution of hierarchical complexity.

At this stage, students are advanced in their understanding of how cooperation between individuals can afect the survival and reproduction of these individuals and of groups of individuals. No matter the specifc individual in question, students would be able to explain how cooperation and division of labor can reduce the workload of any one individual member of the group. Cooperation in groups can increase the ftness of the group members and the ftness (survival and reproduction) of the group. To summarize these points, the lower anchor for this level states: *There are different kinds of biological individuals such as unicellular, multicellular, and social insect colonies. Individuals can form groups and cooperate to increase the likelihood of group survival and reproduction.*

For students to achieve a more complete understanding of ETIs, the next stage of the curriculum sequence must work towards the application of previously learned topics to the understanding of the evolution of the hierarchy of life. Repeated ETIs explain the evolution of the hierarchical organization of life. This understanding is reflected in the upper anchor for this level: *The nested hierarchical organization of life results from the repeated evolution of cooperating groups of individuals into highly integrated groups that are new kinds of individuals*. This is also the upper anchor for the entire scaffolded curriculum sequence.

The key learning outcomes at this stage of the curriculum sequence center on the application of ETI theory to evolutionary concepts. The first two key learning outcomes are the following: (1) natural selection acts on individuals both within and between groups, and (2) natural selection promotes the formation of integrated, cooperating groups of evolutionary individuals. Cooperation and the division of labor between evolutionary individuals proves to be an adaptive behavior that is favored by natural selection, which in turn allows for the physiological integration of groups into evolutionary individuals.

Once students are comfortable with these frst two key learning outcomes, students can continue towards studying the heart of ETI theory itself, the transition in individuality, in the third key learning outcome. Through specialization and division of labor, cooperating evolutionary individuals can become so integrated they would have lower ftness if they were to survive or reproduce *on their own*, and thus the entire group is considered a new individual. This key learning outcome summarizes the crux of ETI theory in addressing the hierarchical organization of life. This hierarchical organization not only refers to the emergence of new species and adaptive diferences between individuals, but also can provide an explanatory framework for hierarchical structure itself as related to cellular functionality. This evolutionary transition in individuality also has consequences for inheritance patterns and cellular division and thus classroom discussions on evolutionary transitions as it relates to inheritance and cellular division will also allow ETI theory to align with NGSS performance expectations related to these concepts.

Lastly, the fourth key learning outcome focuses on the emergence of a nested hierarchy of diferent kinds of individuals resulting from dozens of repeated ETIs over the last 4 billion years. This allows students to gain a sense of the time scale for the evolution of the hierarchical organization of life, thereby incorporating ETIs into student knowledge of macroevolutionary events. As such, through the presentation of these four key learning outcomes, students will be able to obtain an understanding of not only ETI theory by achieving the upper anchor, but to also have a framework for understanding the evolution of the hierarchy of life. These key ideas in this level of the curriculum sequence are summarized in Table [4.](#page-10-0)

It is important to acknowledge what elements of ETI theory have been left out of the upper anchor for this curriculum sequence that remains for more advanced instruction. What has been implicit but not explicit in the curriculum sequence developed here is the multilevel nature of natural selection when individuals are structured into groups. When populations are structured into groups, selection occurs both among individuals within groups and between groups of individuals (Michod [2022](#page-18-17)). Within-group selection means some individuals survive or reproduce better than other individuals within the same group. Between-group selection means that some groups output more ofspring to the next generation than other groups. This multi-level selection is the mechanism by which groups become so integrated that they evolve into a new kind of individual. The multi-level nature of natural selection is left for university level courses in evolution.

Summary

This curriculum sequence for ETI theory provides students with an evolutionary framework for understanding the origin and evolution of hierarchical complexity. In Fig. [2,](#page-2-0) we provide a visual representation and summary of this sequence. Each of the four conceptual levels of the curriculum sequence is represented as a stair in a staircase, where each stair consists of a "rise" and "run." Each "rise" in the staircase represents an increase in sophistication of knowledge, where students progressively obtain a deeper understanding of ETI theory. Each "run" represents the

teaching sequence, presented over time in the classroom, to aid student progression from the lower anchor to the upper anchor. The iterative nature of this curriculum sequence is represented by the joining of each of the "stairs" in vertices. These collective "rises" and "runs" allow for students to progress along a generalized trajectory for obtaining a scientifc understanding of the evolution of complexity through an understanding of ETIs.

By examining this framework as an iterative, stepwise curriculum sequence, instructors can provide a scaffolded approach to teaching the evolution of life's hierarchical organization. Students can start with a generalized, intuitive understanding of the role of groups in biology (i.e., the lowest lower anchor) and, through addressing the key learning outcomes for each level, achieve the scientifc understanding that the nested, hierarchical organization of life is due to repeated ETIs involving evolution of integrated, cooperating groups (i.e., the highest upper anchor). The curriculum sequence makes explicit how to teach the evolution of hierarchical complexity with alignment to the NGSS such that it can be easily incorporated into the local educational context. As the NGSS was developed based on international benchmarks, the curriculum sequence should prove useful in other countries.

Discussion

Teaching hierarchical complexity through ETIs

Hierarchical complexity is taken for granted by the NGSS and by instruction materials and textbooks with limited pedagogical resources to teach its origin and evolution. A student may mistakenly interpret this as a limit as to the breadth and depth of evolutionary theory in its explanation of biological features and provide an opening for non-scientifc explanations of complexity (Behe [1996](#page-17-10); Dembski [2002\)](#page-17-11). The translation of ETI theory into the K-12 biology curriculum, using the internationally inspired NGSS as an example, addresses these concerns. We summarize our arguments here.

ETI theory seeks to understand the evolution of the hierarchical organization of life by asking how groups of cooperating individuals evolve into the new kinds of individuals that constitute the evolutionary levels of increasing complexity present in the hierarchy of life. The theory presents the evolution of hierarchical complexity through the evolution of cooperative interactions which result in increasingly inclusive and nested levels of hierarchical organization. This shift in focus to the evolution of social interactions as the drivers of hierarchical complexity presents the student with a more intuitive approach for understanding evolutionary processes. Students are social individuals and well

equipped to engage both cognitively and emotionally with material based on social interactions. We have presented this framework as a curriculum sequence that is designed to allow students to progressively increase their sophistication of understanding of the evolution of hierarchical complexity. A summary of this curriculum sequence is given in Table [5.](#page-15-0)

Approaches for teaching biological complexity *Complexity in the NGSS*

Complexity is implicit and explicit in several of the science and engineering practices, cross-cutting concepts, and disciplinary core ideas, but the NGSS does not identify complexity, per se, or the evolution of complexity, as teaching goals. Nevertheless, aspects of complexity such as the hierarchy of life do get indirectly taught through the NGSS, especially through its emphasis on levels of organization, even though the levels of organization are taken as a given. For instance, consider the following performance expectations:

- Develop and use a model to describe the function of a cell as a whole and ways the parts of cells contribute to the function (MS-LS1-2).
- Use argument supported by evidence for how the body is a system of interacting subsystems composed on groups of cells (MS-LS1-3).
- Develop and use a model to illustrate the hierarchical organization of interacting systems that provide specifc functions within multicellular organisms (HS-LS1-2).
- Use a model to illustrate the role of cellular division (mitosis) and diferentiation in producing and maintaining complex organisms (HS-LS1-4).

Each of the NGSS performance expectations above requires students to take these complex systems and levels of organization for granted with no mention as to their origin or evolution. This is further supported by the omission of the evolution and complexity in the cross-cutting concepts of 'system and system models' and 'structure and function' and the disciplinary core ideas of LS1.A (structure and function), LS1.B (growth and development), as well as the omission of complexity in the entire disciplinary core idea of LS4 (evolutionary biology). As a result, complexity is a topic missing from summaries of content (Ziadie and Andrews [2018](#page-19-0), [2019](#page-19-1)). The lack of explicit attention to the evolution of complexity in these key areas in the dimensions of the NGSS is alleviated by the inclusion of concepts from ETI theory.

Complex systems approach

Education researchers have proposed taking a complex systems approach for teaching and learning strategies on biological complexity (Verhoeff et al. [2013](#page-18-34), [2018](#page-18-35); Yoon et al. [2018](#page-19-2)). Complex systems have been predominantly taught with respect to levels of biological organization (Asshoff et al. [2020;](#page-17-17) Gilissen et al. [2021](#page-17-18); Jördens et al. [2016](#page-17-19); Schneeweiß and Gropengießer [2019;](#page-18-36) Wilensky and Resnick [1999](#page-19-3)) and systems thinking with consideration of the emergent properties of these systems (Jacobson and Wilensky [2006](#page-17-20); Penner [2000;](#page-18-37) Wilensky and Resnick [1999](#page-19-3)). This has led to the development of several teaching and learning strategies that focus on a systemsthinking approach, such as agent-based modelling approaches with computer simulations such as NetLogo (Wilensky and Reisman [2010\)](#page-18-38), classroom activities with manipulatives to aid in thinking about levels of organization (Jördens et al. [2018\)](#page-18-39), yo–yo learning (Knippels and Waarlo [2018;](#page-18-40) Knippels [2002\)](#page-18-41), and zoom maps (Schneeweiß and Gropengießer [2022](#page-18-42)). There have also been investigations on how to systematize learning about complex systems through learning progressions (Yoon et al. [2019](#page-19-4)) and unifying conceptual frameworks centered around systems and systems thinking (Momsen et al. [2022\)](#page-18-43).

We agree that complex systems thinking is useful and helpful in understanding properties of biological complexity. However, the emphasis in this complex systems approach and associated instructional materials is on understanding properties of the system, not on explaining and understanding how the system originated and evolved to have these complex properties. ETI theory is still needed for understanding the origin and evolution of the complex system.

Implications for evolution acceptance

The inclusion of explicit instruction on the origin and evolution of biological complexity through teaching hierarchical organization should have consequences for evolution acceptance. Currently, students are not taught the background needed to understand the evolution of hierarchical complexity. This gap in instruction contributes to a lack of understanding that evolution does, indeed, explain the increasingly complex levels present in the hierarchy of life. This lack of instruction, even after standard lessons on evolution, does not allow the student to give an educated response to questions that are currently being used in various measures of evolution acceptance, as explained below. This means the student will provide a response that refects their evolution knowledge rather than evolution acceptance. Evolution knowledge refers to students' understanding of basic evolutionary concepts, such as natural selection (Anderson et al. [2002](#page-17-21)) and tree thinking (Jenkins et al. [2022](#page-17-22)), whereas evolution acceptance refers to whether the student agrees that the principles of evolutionary biology can explain the diversity of life. If students are not taught how hierarchical complexity evolved how can they know if they accept evolutionary biology as an adequate explanation for the diversity of life? This gap in instruction then adds to the complexities of interpreting results from evolution acceptance studies (Barnes et al. [2019](#page-17-23); Kuschmierz et al. [2020\)](#page-18-44). By explicitly addressing the evolution of biological complexity in the classroom, more accurate responses can be provided to these measures of evolution acceptance.

The measurement of evolution acceptance has been studied resulting in published surveys and each of these surveys includes items related to biological complexity. For example, in the Inventory for Student Evolution Acceptance (I-SEA), Nadelson and Southerland ([2012](#page-18-45)) ask respondents to assign their level of acceptance via a Likert scale to the following statements: (a) I think all complex organisms evolved from single celled organisms, and (b) I think that the physical structures of humans are too complex to have evolved. The Evolutionary Attitudes and Literacy Survey (EALS) (Hawley et al. [2011;](#page-17-24) Short and Hawley [2012\)](#page-18-46) asks respondents to respond to the following statements: (a) Complex biological systems cannot come about by slight successive modifcations, and (b) Natural selection cannot create complex structures; it is like a tornado blowing through a junkyard and creating a 747. These references to biological complexity in surveys of evolution acceptance indicate that student perception on whether evolutionary biology has the capacity to explain complexity afects their acceptance of evolution. However, as shown here, current instruction and curriculum paradigms including the NGSS do not adequately prepare students to address these questions that occur in the measures of acceptance.

Conclusions

The living world is hierarchically complex but the evolution of the hierarchy of life and complexity per se are not topics usually presented in the biology classroom. Hierarchical structure and complexity are implicit in many of the NGSS performance expectations and there is a developing education literature on teaching complex systems. However, the NGSS standards and education literature take the complex system for granted, they do not address how the system evolved in the frst place and how it evolved to be hierarchically structured with distinct levels of complexity. We seek to fll this gap in instruction by translating ETI-related research into instructional materials by aligning the core concepts

and principles of ETI theory to the NGSS disciplinary core ideas, cross-cutting concepts, and science and engineering practices. Through the materials presented here, students should be able to understand that groups of cooperating individuals can evolve into new kinds of individuals, and that this process has happened recursively to give rise to the hierarchy of life we know today with its levels representing major landmarks of biological complexity. Teaching the hierarchy of life using ETIs leverages the familiarity students have with social interactions in their lives to understand life's biological diversity and complexity.

Supplementary Information

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Additional fle 1.

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Author contributions

All authors contributed equally to the writing of the manuscript. Following the CRediT guidelines (located here: [https://www.elsevier.com/resea](https://www.elsevier.com/researcher/author/policies-and-guidelines/credit-author-statement) [rcher/author/policies-and-guidelines/credit-author-statement](https://www.elsevier.com/researcher/author/policies-and-guidelines/credit-author-statement)) the author contributions are as follows. Hoskinson: Conceptualization, Methodology, Visualization, Writing - Original Draft, Writing - Review & Editing; Davison: Conceptualization, Methodology, Visualization, Writing - Original Draft, Writing - Review & Editing, Funding Acquisition; Sanders: Conceptualization, Methodology, Writing - Original Draft; Jimenez-Marin: Writing - Review & Editing; Michod: Conceptualization, Methodology, Visualization, Writing - Original Draft, Writing - Review & Editing, Funding Acquisition, Project Administration, Supervision.

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No datasets were generated or analysed during the current study.

Declarations

Competing interests

The authors declare no competing interests.

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