Translating research on evolutionary transitions into the teaching of biological complexity

Running title. Teaching biological complexity
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Please tell us in 50 words or less how your study advances the field of evolutionary biology.

We translate recent research on evolutionary transitions in individuality into the teaching of biological complexity and the evolution of the hierarchy of life. These topics had been left out of the curriculum with negative effects on the public's understanding of and engagement with evolutionary biology.

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Abstract

(200 words)
Nested hierarchical structure is one of life's most familiar properties and a major component of biological diversity and complexity. However, there is little effort to teach the evolution of the hierarchy of life, as there is little effort to teach biological complexity per se. We propose a framework for teaching biological complexity based on research on evolutionary transitions in individuality (ETI theory). Translating ETI theory into the classroom allows students to see the connections between natural selection, social behavior in groups, and the major landmarks of biodiversity in the hierarchy of life. The translation of ETI theory into pedagogic content and practices involves (i) the new content that must be taught, (ii) the development of general teaching tools to teach this new content and (iii) connecting the new content and teaching tools to the specific educational context including integrating with learning standards and benchmarks. We show how teaching ETIs aid in the teaching of science practices and in teaching the process of evolutionary change. Evolutionary transitions research provides a way to teach biological complexity that is familiar and engaging to students, leveraging their inherent understanding of social dynamics and group behavior.

Keywords

Biological complexity, individuality, evolutionary transitions, science practices, Next Generation Science Standards, K-12 education

Introduction

Complexity is inherent in most biological phenomena, yet complexity does not appear as a topic by itself, per se, in the biology classroom. This omission has had negative consequences for biological instruction and for the public's understanding of the origins and evolution of biological complexity, providing an opening for nonscientific theories of complexity. Life began simple so it is not surprising that it became more complex. What is remarkable is *how* life became more complex and the hierarchically structured way in which biodiversity is organized on earth. The living world today, more than 3.5 billion years after life first originated on the planet, is a nested hierarchy of different kinds of evolutionary individuals: genes, cooperative networks of genes or genomes, simple cells, complex eukaryotic cells, multicellular organisms, and eusocial societies (Figure 1). Explaining this complexity has been a major achievement of evolutionary biology in the last fifty years and how we might teach this complexity is the major goal of this paper.

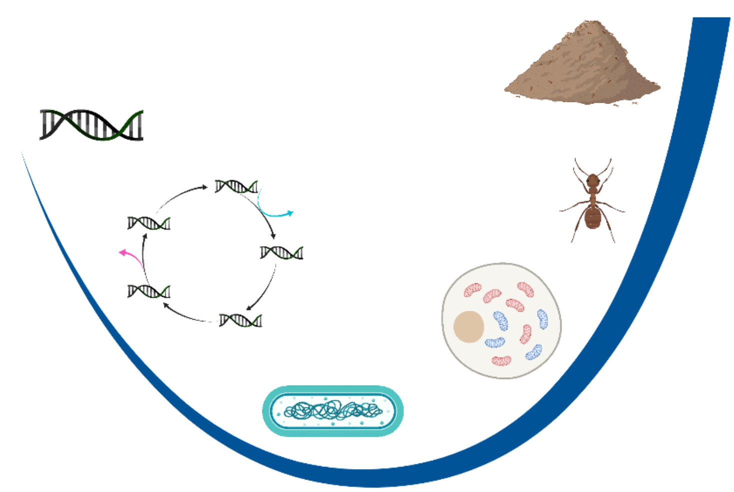

Figure 1. Life's nested hierarchical structure of different kinds of evolutionary individuals. The levels depicted are genes, cooperative gene networks or the first genome, bacteria-like cells, complex eukaryotic cells, multicellular organisms (could be comprised of either bacterial or eukaryotic cells), and eusocial societies (e.g., an ant colony mound). The ant depicted in the figure is assumed to be from a solitary ant species. That is, it is a multicellular individual, unlike ants that are members of eusocial insect colonies which are specialized parts of the colony level individual. Created with biorender.com.

Individuals are central to evolutionary biology because natural selection acts on individuals and we must identify and count individuals when studying evolution. Different kinds of individuals have different degrees of complexity as measured by their number of parts, degree of integration, or nestedness. The hierarchical structure of nested levels of individuality is one of life's most familiar properties and is presented in figure form at the beginning of many biology textbooks. Since the hierarchical structure was not present at the origin of life, scientists must explain, and students must understand, how it has arisen over the course of evolution.

Each level in the hierarchy of life is comprised of individuals present at a previous level, yet these prior individuals have become mere parts of a larger, more complex, and new kind of evolutionary individual (Figure 1). Evolutionary transitions in individuality, or ETIs, refer to the process by which new kinds of individuals evolve from groups of pre-existing individuals. Repeated ETIs are hypothesized to have bestowed on life its hierarchical structure of nested evolutionary individuals.

In this paper, we seek to translate our understanding of the science of evolutionary transitions research (ETI theory) into the teaching of the evolution of biological complexity. We propose ways in which ETI theory may be used to increase student understanding of and engagement with evolutionary biology generally. This work converges with other science education reforms that have been ongoing in the United States and internationally in primary and secondary education (DeBoer, 2000; Pea & Collins, 2008; Woodin, Celeste Carter, & Fletcher, 2010) and undergraduate biology education (Woodin et al., 2010).

Our paper is organized around the following points. Understanding the evolution of complexity per se is important for a basic understanding of biology. However, there is not much that is currently being done to teach the evolution of biological complexity per se in schools. We propose a framework for the teaching of biological complexity based on evolutionary transitions research and the origin of new kinds of evolutionary individuals that underpin the hierarchy of life (ETI theory).

We translate ETI theory into pedagogic content and practices. Our translation framework involves three considerations that facilitate the incorporation of research into educational practice: (i) identification and subsequent description of the new content that must be taught, (ii) the development of teaching tools to teach this new content, including materials, activities, teaching scaffolds, and analogies that are useful in the classroom, and (iii) connecting the content and teaching tools with the local educational context.

The instructional content involves three areas: individuality as a core concept, cooperation in social groups, and the hierarchy of life. We provide five tools for teaching this content that may be adapted to different levels of instruction and different educational contexts. We illustrate these tools using two examples based on our experiences teaching evolutionary biology in the United States at the middle school and university levels. Our framework is flexible and can be adapted to educational contexts within the United States and internationally, across primary and secondary education. We begin by giving a brief overview of ETI theory.

Evolutionary transitions in individuality research – an overview

All fields of science must define and explain their most basic individual units. In evolutionary biology, this unit is the evolutionary individual. Evolutionary individuals must have heritable variation in fitness, which is necessary for natural selection to occur. Fitness has two components: survival and reproduction. Biological individuals both survive and reproduce by themselves at their level of organization. For example, cells in a multicellular organism are not individuals, since they do not both survive and reproduce offspring by themselves. Even a germ cell is not an individual since it cannot survive on its own. However, in unicellular organisms, cells are individuals since a single cell can both survive and reproduce the organism. Evolutionary biologists identify and count individuals when studying how populations change over time. If we are studying the evolution of antibiotic resistance in a bacterial population, we count cells and record their traits, and if we are studying the evolution of beak size in birds, we count not cells but birds, again recording their traits.

ETI theory seeks to mathematically model and explain how groups of individuals evolve into the new kinds of individuals that make up the hierarchy of life. Individuals at each level in life's hierarchy are comprised as groups of individuals from the previous level, so ETI theory hypothesizes that each level originates as a group of previously existing individuals (Figure 1). There are several reviews and overviews of ETIs (Hanschen, Davison, Grochau-Wright, & Michod, 2018; Michod, 2007a; West, Fisher, Gardner, & Kiers, 2015). We use the framework of ETIs developed by Michod and colleagues (Hanschen, Shelton, & Michod, 2015; Michod, 1999, 2007b, 2021), although the teaching points made apply to evolutionary transitions research generally. This work is an extension of research into evolutionary individuality begun by Buss (1987) and Maynard Smith (1988, 1991), and subsequently developed by Maynard Smith and Szathmáry in their landmark book (1995). The work of Buss, Maynard Smith, and Szathmáry (op. cit.) was made possible because of the revolution in evolutionary social behavior theory that occurred in the 1970s in which social principles were applied to the different levels of biological organization, including molecules and cells (Eigen & Schuster, 1977; Hamilton, 1975; Wilson, 1975).

ETIs proceed through several stages, beginning with the formation of groups of individuals (Hanschen et al., 2018; Michod & Nedelcu, 2004). Group formation may occur for a variety of reasons, for example, in the case of the evolution of multicellularity, daughter cells may stick together after cell division, producing a group of genetically-related cells. In the case of the evolution of the eukaryotic cell, groups of bacterial and archaeal cells may form cross-feeding aggregates. After groups form, increased cooperation may evolve among members of the group. The evolution of cooperation leads to the evolution of conflict (cheating). Under certain conditions, conflict mediating mechanisms evolve. Conflict mediators are group traits that promote cooperation and restrict the opportunity for the origin and spread of selfish behaviors. Examples of conflict mediators include, in the case of multicellularity, a sequestered germline separate from the somatic cell lineage and cell policing like happens with the immune system.

Conflict mediation can lead to the evolution of a division of labor in the basic components of fitness: survival and reproduction. If group members evolve that specialize in reproduction and other group members specialize in traits promoting survival, the opportunities to cheat are restricted. Group members specialized in reproduction or survival are missing the other essential component of fitness. Since evolutionary individuals must be able to both survive and reproduce, specialized group members are no longer an evolutionary individual by themselves. They can no longer survive and reproduce by themselves. As a result, division of labor or specialization by group members in the basic components of fitness survival and reproduction would decrease the fitness of the members, if they were to exist alone, but this specialization may increase the fitness of the group. The fitness of the group may be quite high, even though members of the group may not survive or reproduce outside of the group context. This transfer or decoupling of fitness of the group from the fitness of its members along with heritability of group fitness is the final stage of an ETI.

What new content is needed to teach complexity and ETIs?

Overview

The first step in translating research into practice, is to identify relevant scientific knowledge that is missing or necessary (Gagnier & Fisher, 2020). Bridging ETI theory and the teaching of biological complexity requires the consideration of three topical areas: (1) *individuality as a core concept in biology*, (2) *cooperation and natural selection in social groups,* and (3) *the hierarchical organization of biological diversity*. The logic underlying and connecting these three content areas is general and based on research on evolutionary transitions. Cooperation evolves in social groups because it allows for groups to function in ways that are unavailable to solitary individuals (topic 2). The continued evolution of cooperation in social groups (topic 2) may lead to such a high degree of cooperation and integration in a group that the group evolves into a new kind of individual (topic 1). This process has happened multiple times during the history of life on earth to produce the hierarchy of life as we see it today (topic 3).

These three content areas are not completely new and not all content areas are developmentally appropriate for all grade levels. What is required is new connections between key concepts already being taught, along with a continuation of specific key concepts related to individuality, sociality, and group behavior throughout a student's education. The details of the content must also be scaffolded throughout the educational trajectory in an age and stage-specific way.

Individuality

Evolutionary individuals survive and reproduce by themselves, but under some conditions, individuals live in social groups. ETI theory involves the study of cooperation and natural selection in social groups and the ways in which social groups may become so integrated they evolve into a new kind of individual. Biological individuals have the Darwinian characteristics of heritable variation in fitness that underlie natural selection. ETI theory is a theory of fitness, the components of fitness, and how these components are reorganized as selection moves from the level of the individual to the level of the group to the level of a new kind of individual. The two basic components of fitness, survival and reproduction, often trade-off with one another. Resources invested in one component, say survival, decrease the other component, say reproduction. These trade-offs between fitness components are leveraged during ETIs to create division of labor in the group. As individuals specialize in the different components of fitness of the group, the heritability of fitness can move from the individual level to the level of the group.

Cooperation

Natural selection is usually taught in the context of solitary organisms, leading to an emphasis on competition and survival of the fittest. Many organisms live in groups, so the second area of emphasis in instruction is adaptation in social groups with its focus on the evolution of cooperation and its central problem cheating. Cooperation and the mediation of cheating are important driving forces behind ETIs. The opportunity for cheating is the major problem that must be addressed during the evolution of individuality. This problem can be addressed through the evolution of conflict mediating mechanisms, which are group properties that restrict the opportunity for members to cheat. Students are aware of these properties, because conflict mediating mechanisms exist in every social group they belong to, including the classroom and society generally. Consider, for example, the many institutions in human societies such as rules, laws, and police forces that restrict the opportunity to cheat and encourage cooperation. Similar group traits exist in other organisms that live in groups. When considering the large-scale patterns of biological diversity as represented in the hierarchy of life, cooperation in groups and the mediation of conflict are central driving forces.

Hierarchy of life

The hierarchy of life is the overarching framework for biological complexity and represented in figure form in most biology textbooks. In his review of biological education research, Nehm (2019) recognizes the value in using the hierarchy of life as a unifying framework to teach biology, but states that "a review of the literature reveals that an explicit curriculum for helping students engage in the meaning of this hierarchical arrangement appears lacking." Dauer and Dauer (2016) argue that understanding hierarchical organization "…is a major challenge for advancing twenty-first-century biology and for preparing undergraduate students to address difficult issues that our society faces." They further argue that this challenge "…is expressed in different ways throughout primary and secondary standards in the USA and post-secondary education, both generally in terms of sequences of increasing sophistication across grade bands and specifically in terms of concepts that students should master." ETIs provide the basis for the missing curriculum needed for students to engage with life's hierarchical organization and for understanding the origins and manifestation of biological complexity.

In the United States, biodiversity is usually taught using a comparative taxonomic approach (e.g., Glencoe Science, 2017), comparing the life cycles and traits of different taxonomic groups, such as animals, plants, protists, and bacteria. There is little in the way of an overarching framework. Teaching phylogeny and tree-building are becoming more commonplace at the middle school and high school levels (Catley & Novick, 2008) and at the university (Smith & Cheruvelil, 2008), but students are not being taught the structural rules of trees and their theoretical underpinnings (Catley & Novick, 2008). The lack of a conceptual framework in the classroom leads to the memorization of facts as the main student activity. This memorization can be a slog for students and lead's to decreased engagement.

The hierarchy of life can be used as an overarching framework for the comparative, taxonomic, and phylogenetic approaches to teaching biodiversity. ETIs offer a rich conceptual framework for explaining life's hierarchical organization based on social principles driven by a simple question, why do groups of individuals become individuals. As already mentioned, human beings are social animals, we have evolved to engage both emotively and cognitively with social factors. As a result, we may expect engagement with ETIs and the complexity of life, especially when the principles underlying ETIs are modeled in the classroom which is itself a social group. This leads to the new teaching tools that are helpful in teaching ETIs.

Teaching tools to support the translation of ETIs into teaching biology

Overview

The second step in translating scientific research into the classroom is the development of teaching tools to increase student understanding of and engagement with the new areas and new content (Gagnier & Fisher, 2020) . Teaching tools support teachers' pedagogy, that is, the methods and strategies by which teachers convey knowledge to facilitate students' deeper understanding of content. Teaching tools include the materials teachers use to support the presentation of content and other resources and activities utilized in the classroom. Teaching tools may also include the development of analogies between what the students already know and the new content.

We provide five teaching tools that are especially useful in teaching ETIs that may be implemented in a variety of contexts and levels of instruction. Examples of implementations of these tools in middle school and university are given in the next section. The tools for teaching ETIs include (i) analogies between the social lives of students in and out of class and the social groups of evolutionary individuals during an ETI, (ii) cooperation games that may be played in the classroom to teach cooperation and strategies for mediating conflict, (iii) labs and exercises based on a model system for studying complexity (the green algae *Volvox* and its relatives introduced in Figure 2 below), (iv) guided classroom discussion of "what is life?" leading to a focus on survival and reproduction of individuals as embodied in the question, can it survive and reproduce by itself? and (v) phylogenetic tree building and tree thinking.

Analogies

There are two general analogies that can be made in teaching ETIs that are useful in any context: (i) the analogy between the dynamics of the classroom as a social group and the dynamics of social groups during an ETI, and (ii) the analogy between the social lives of students and the social behavior of individuals in evolutionary groups during ETIs. Teaching practices built on these two analogies naturally harness the power of analogical reasoning, (Gentner & Smith, 2012; Goswami, 2013) a tried-and-true companion of sound teaching (Vendetti, Matlen, Richland, & Bunge, 2015).

The classroom is a social group and can be used to model the principles and stages involved in the conversion of a group of individuals into a new kind of individual. The stages in an ETI discussed above are group formation, cooperation, conflict, mediation of conflict, division of labor, and transfer (or export) of fitness from the individual to the group. These stages that ETIs are theorized to go through, bear a striking resemblance to a theory put forth by Tuckman (Tuckman, 1965; Tuckman & Jensen, 1977) that describes the stages that small human groups go through when they are asked to solve problems or perform new tasks. Tuckman's stages are (with the corresponding ETI stage in parenthesis) forming or testing-dependence (group formation and cooperation), conflict (conflict), cohesion (conflict mediation), and functional roles (division of labor). The correspondence is not one-to-one and there is some overlap between stages, but still, it is interesting that groups of human individuals and groups of evolutionary individuals are hypothesized to go through similar stages when developing or evolving as a group. The human group stages can be modeled in the classroom following a variety of online tools (e.g., MindTools, 2021; Multi-Stakeholder & Partnerships, 2021) and the correspondence of the observed student group stages to the ETI stages discussed with students. The final stage of fitness transfer in an ETI is not reflected in the human social group dynamics and Tuckman's principles, because the social group in Tuckman's case has a functional task, not a self-reproductive one.

The second analogy that is useful in teaching ETIs is the analogy between the social lives of students both in and outside of the classroom and the social behavior of evolutionary individuals in groups during ETIs. Students are personally aware of the benefits of cooperation as well as the temptation to cheat in their social lives. Human beings evolved as social animals and are well equipped both emotively and cognitively to engage with social principles and content. Childhood organizes a child's intuitive understanding of the functioning and organization of social groups, so even in the youngest classrooms, this analogy should prove helpful in preparing for the teaching of evolutionary transitions at later stages (Hirschfeld, 2016). The youngest students can appreciate the benefit of sharing and group membership (Olson & Spelke, 2008).

Cooperation games

The benefits and costs of cooperation may be taught through games played in the classroom. These games typically involve a benefit of cooperating with others along with a temptation to cheat. The specific games employed depend on the level of instruction and age of the students along with the specific aspects of cooperation that are being taught. This is discussed in more detail below in the two cases studies given for middle school and university levels. In using games in the classroom, we follow the advice of Mayer (2016) who after reviewing the role of computer games in education concluded "Policy implications are to use games for targeted learning objectives, align games with classroom activities, avoid confusing liking with learning, and use games to adapt activities to maintain challenge."

Volvocine green algae as a model system

Scientists use various tools to see outside their "normal" biology-based spatial and temporal frames of reference. For example, science addresses very small phenomena that we cannot see with our unaided eye as well as phenomena that occur over very short or long-time scales that are outside of our frame of reference. To address and explain such phenomena, scientists use tools such as diagrams, microscopes, mathematical models, and model systems. Likewise, teachers may employ similar tools that can expand a student's understanding into temporal and spatial scales that are outside their normal frame of reference.

ETIs are rare events, having happened only dozens of times, and outside of our normal frame of reference. How can students visualize and understand the intermediate stages predicted by ETI theory? The volvocine lineage of unicellular, colonial, and multicellular forms is a tool for seeing and teaching the intermediate forms predicted by ETI theory in the case of the evolution of multicellularity from unicellular ancestors (Figure 2).

The volvocine green algae (*Volvox* and its close relatives) are a model system for understanding the evolution of complexity and the origins of multicellularity and are fascinating because of their diverse forms based on repeated structures (Kirk, 1998a; Michod, 2007c; Nishii & Miller, 2010). The multicellular forms in panels B-D in Figure 2 diverged from unicellular ancestors similar to panel A around 220 million years ago (Herron, Hackett, Aylward, & Michod, 2009; Herron & Michod, 2008). The large, complex forms such as *Volvox* in panel D still coexist with smaller, less complex forms (panels A-C) in ponds and freshwater habitats around the world. This diversity and recent evolution of multicellularity (compared to multicellular animals and plants) make the volvocine algae ideal for understanding the genomic, morphological, and developmental changes by which a single-celled organism can evolve into a more complex, multicellular one. These algae are readily available through biological supply houses and can also be easily collected by students from freshwater ponds and lakes around the world. While our presentation of volvocine green algae is geared towards ETI theory and the evolution of multicellularity, these algae can also be used for instruction in ecology and general biology at younger age levels (Nozaki, 2000).

Four species representing the morphological diversity of the volvocine algae are shown in Figure 2. Panel A is *C. reinhardtii*, an extant unicellular species inferred to be similar to the unicellular ancestor of the volvocine clade using phylogenetic, comparative and genomic methods (Featherston et al., 2018; Hanschen et al., 2016; Herron et al., 2009; Herron & Michod, 2008; Kirk, 1998b; Merchant et al., 2007; Prochnik, Umen, & Nedelcu, 2010). *Volvox carteri* is one of the more complex multicellular species in the lineage, having two kinds of specialized cell types: germ and soma (small and large cells in Figure 2 panel D). There are a variety of intermediate species in between the unicellular *C. reinhardtii* and the multicellular *Volvox* in body size and complexity. Two examples are given in Figure 2. In panel B is the 16-celled *E. elegans* that typically has only one kind of cell: an undifferentiated, general-purpose *Chlamydomonas*-like cell. Like a *Chlamydomonas* cell in panel A, these undifferentiated cells begin life with flagella that help in motility and then lose their flagella to divide and reproduce. In panel C is the 64-celled *Pleodorina starrii*; this species has two kinds of cells, undifferentiated cells like in *Eudorina elegans* and the smaller-sized somatic cells that keep their flagella throughout the life cycle.

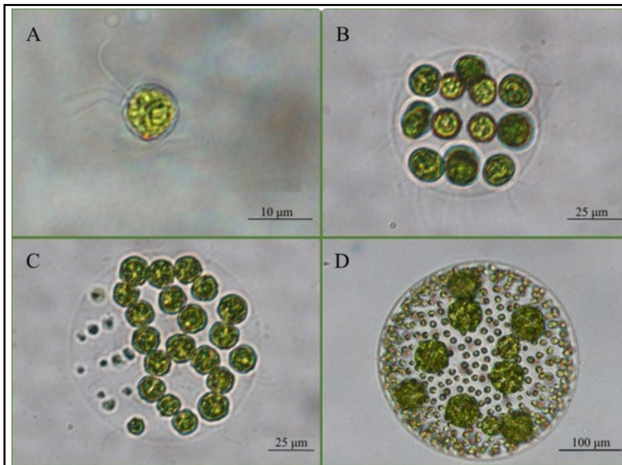

Figure 2. Volvocine green algae. (A) *Unicellular Chlamydomonas reinhardtii* strain CC 124. (B) *Eudorina elegans* strain UTEX 1201, in which member cells are typically undifferentiated, but cooperate in flagellar action and building a structured spherical colony with a colony boundary. (C) *Pleodorina starrii* strain NIES 1362, which possesses both undifferentiated cells and small (to the left in the picture) somatic cells that do not reproduce and specialize in flagellar action and survival. (D) *Volvox carteri* strain Eve, which consists of large germ cells (10 such cells are visible in the picture) specializing in reproduction and small permanently flagellated somatic cells specializing in survival.

These species can be used to teach about the evolution of complexity during the evolutionary transition from unicellular to multicellular life. They have been inferred to be like the intermediate forms arising in the evolutionary past that led from an ancestor looking like the species in panel A to the descendant multicellular species in panel D, through intermediate stages, some of which are predicted to be like the species shown in B and C. Thus, the extant volvocine species are a tool for seeing the intermediate forms that existed millions of years ago during the ETI in this lineage.

Guided classroom discussions of life and individuality

Can it survive and reproduce on its own? is a guiding question for students to first think about individuality. Biology classes at all levels often include a discussion of what it means to be alive. This is a good time to introduce the topic of individuality (even if only obliquely at young age levels without specifically mentioning the term "individuality"). Individuals are alive because they survive and reproduce by themselves, unlike parts of individuals (specialized cells which require the whole organism to reproduce into the next generation), and unlike collections of individuals (communities or ecosystems which do not reproduce as a unit). As students are introduced to new biological entities and forms during the year they may return to this guiding question, can it survive and reproduce on its own, at its level of organization, that is, is it an individual?

Tree thinking

The building of phylogenetic trees is useful in any evolutionary context, but for the teaching of evolutionary transitions, tree thinking has special uses. It provides a framework for discussing the intermediate stages in an ETI and the traits predicted to be in these ancestors that connect an individual (like a cell) to a new kind of individual (like a multicellular organism). Tree thinking may also be used to visualize the merger of the genes and genomes from different lineages that occurred during the so-called 'egalitarian' ETIs (Queller, 1997). In egalitarian transitions, groups are formed by symbiosis of different species instead of by cells or products of replication staying together after division. Examples of egalitarian transitions are the origin of the eukaryotic cell from the formation of groups of bacterial and archaeal cells, or the formation of hypercycles (groups of cooperating genes) during the evolution of the genome.

Adapting and integrating the new material into the local education context

Overview

The third issue to address when translating research into the classroom is how to map the new content into the local education context in which the teachers are working. This involves a variety of issues including the age and grade of instruction, prerequisites, standards, or benchmarks expected at the level of instruction and subsequent levels, and existing curriculum that may need to be included or modified. There may also be cultural issues and issues related to the kind of school (public, private, or parochial) in which the new content is being incorporated.

Barriers to the translation of research into the classroom arise when “translators” fail to understand and address the learning needs, resources, and interests of the local school or education context (Gagnier & Fisher, 2020). The most impactful and meaningful translation occurs through working closely with educational partners (teachers, school leaders, curriculum developers) throughout the translation process. Their expertise, professional knowledge, understanding of the local context is imperative to the success of the translation.

As already mentioned, getting to know the local education context involves a variety of issues. We consider two in more detail: (1) existing learning standards or benchmarks and (2) curriculum. In both cases, we are primarily interested in how the new content and teaching tools discussed above may be integrated. We consider two case studies based on our experiences with teaching evolutionary biology in the United States at middle school (ages 10-14) and university levels.

Existing standards or benchmarks set expectations for what students should be able to know and do following instruction. There may also be prerequisites to instruction that need to be addressed. For example, in the United States in 2012 the National Research Council released a new framework (NRC, 2012) and associated expectations for what students should be able to know and do from kindergarten (ages 5-6) to high school (ages 14-18) in science. These Next Generation Science Standards, or NGSS for short, were developed in the United States based on international benchmarking of 10 countries that were deemed more advanced in the instruction of science and math than was the United States at that time (Canada [Ontario], Chinese Taipei, England, Finland, Hong Kong, Hungary, Ireland, Japan, Singapore, South Korea) (NGSS, 2010). Consequently, while the NGSS are specific to the United States, they are reflective of the international expectations high-performing countries have set for their students.

The internationally-inspired NGSS are designed to help students develop a cohesive understanding of disciplinary core ideas, cross-cutting concepts, and scientific practices through active learning experiences (National Research Council, 2012). Currently, over 70% of U.S. students have their science curriculum aligned with the NGSS (National Research Council, 2012; NGSS, 2013)(NSTA, 2021), so it is critical for us to align new content and tools to these standards. In a follow-up paper, we give more detail about how ETIs help teach the NGSS.

The NGSS provide detailed expectations and scaffolding of instruction for grades K-12 or ages 5-18. There is less uniformity of standards and prerequisites at the university level, at least in the United States. Recognizing this, the American Association for the Advancement of Science or AAAS developed a "Vision and Change" document for instruction of biology at the university level

(AAAS, 2011), but this document is less detailed and not as widely followed as are the NGSS for K-12.

The second issue to consider when adapting and integrating new material into the local classroom is the existing curriculum. By curriculum, we mean planned experiences designed to help students practice and achieve mastery of knowledge and skills. The curriculum can be understood as any learning sequence designed to enhance student learning and facilitate teachers' instruction; this can include commercially available curricula or educator-designed activities. Understanding the curriculum involves asking questions such as, what content is already included in the existing curriculum and how does it map onto the three additional content areas outlined above (individuality as a core concept in biology, natural selection and adaptation in social groups, the hierarchical organization of biodiversity)? Does the curriculum include any tools which can be adapted to the new material rather than developed materials from scratch? Are there specific lessons or units in which the new ETI content will be most appropriate to be translated?

In sum, the goal of this third translational step involves understanding how ETI content and tools will be developed, adapted, and implemented within a specific educational context. We consider in more detail two contexts from our experiences teaching evolutionary biology in the United States: middle school (sometimes called junior high school, grades 6-8, ages approximately 11 - 14) and university-level teaching in an introductory biology class and in a more advanced course devoted to evolutionary biology. In both cases, we have developed interventions based on the tools introduced above: the use of analogies between ETIs and the social group dynamics in the classroom and the social lives of students, the use of volvocine green algae as a model system, the use of cooperation games in the classroom, the focus on survival and reproduction and characteristics of life in the teaching of biological individuality, and tree thinking.

Example 1: Middle School

Overview of middle school

Middle school biology in the United States often begins by introducing and describing the characteristics of living organisms and studying how they are categorized (Glencoe Science, 2017). This progresses into a discussion of cells, their structure and function, and their reproduction. From here, students learn about genetics, mutations, and how organisms change over time. After the evolution unit, students study the various phyla, usually starting with simple organisms and ending the school year with more complex organisms.

As noted previously, there are three topics or content areas involved in our translation of ETI research into the teaching of biological complexity: (i) individuality, (ii) cooperation and natural selection in social groups, and (iii) the hierarchy of life. Again, the logic connecting these topics is that (ii) cooperation in groups may lead to the evolution of (i) new kinds of individuals and that this process has happened dozens of times to (iii) produce the levels of complexity present in the hierarchy of life today. We have been teaching these topics through implementing the six general teaching tools introduced in the last main section. The implementation of each tool aims to improve student understanding of, and engagement with, evolutionary biology generally and specifically with regards to the subject of biological complexity, a topic missing from summaries of content in the evolution K-12 classroom (Ziadie & Andrews, 2018, 2019).

Analogies of ETIs to student social groups

The value in playing cooperation games discussed next is based on an analogy between human groups and ETIs. As discussed above, the stages in an ETI mirror Tuckman's four stages that small human groups proceed through in problem-solving. The classroom is a social group and so can be used to mirror these stages. Our inclusion of a cooperation game in the classroom proceeds through Tuckman's four stages. In this way, we introduce middle school students to the subject of group cooperation, so they are better prepared to use group behavior to mechanistically explain the evolution of new kinds of individuals in high school biology. Studying cooperation in groups in middle school provides students with foundational knowledge on division of labor and collaboration which is important to understanding the mechanisms underlying ETIs in high school and college.

Cooperation games

We introduce the evolution of cooperation to middle school students through playing the popular cooperative learning game "Among Us" (Innersloth, 2018). We follow the advice of Mayer (2016) in using games in the classroom and specify explicit learning objectives in playing the game. After playing the game students will be able to (i) define cooperation and division of labor, (ii) explain why cooperation and division of labor are beneficial to group members' survival, (iii) discuss the benefits of communication in a group, and (iv) identify examples of cooperation, division of labor, and communication in nature.

When playing Among Us (Innersloth, 2018), students are placed into groups and randomly assigned to be an imposter or a crewmate. Crewmates complete tasks and work together to determine who the imposter is; the imposter eliminates the crewmates while pretending to be a crewmate themselves. Students learn about cooperation and collaboration in two ways: they collaborate about who the imposter could be, and they complete complementary tasks to win. The first way teaches them about how it is easier to discover who the imposter is when they can collaborate and communicate with one another. The latter teaches them about division of labor, since the tasks can be completed much more quickly when students divide them up, thereby specializing on different tasks, than if they each had to complete all the tasks. Ultimately, this game and associated activities teach students one critical concept - that cooperative groups can accomplish tasks and activities that individuals alone cannot.

The focus on cooperation is a fundamental shift in the biology classroom. Without the inclusion of individuality and the evolution of cooperation in social groups, the teaching of natural selection is only competition-based, focusing on the survival of the fittest and the fight for resources.

Volvocine algae as a model system

We have implemented the volvocine green algae model (Figure 2) in the form of laboratory exercises to teach about the gene, cell and multicellular levels present in the hierarchy of life, the benefits of cooperation and large body size, and the stages present during an ETI. These exercises are refinements of the volvocine green algae tools we have developed for the teaching of biological complexity in high school (Farr, Herron, Michod, & Steves, 2009) and are based in part on the multicellularity lab developed by Pentz et al. (2015). The multicellular algae *Volvox* and its relatives are readily available for use in the classroom. Our lab activities are available upon request from the authors.

One goal of our lab is to help students connect what they learned about cooperation from the Among Us game (Innersloth, 2018) to their understanding of individuality, which is centered on survival and reproduction. Students start by characterizing the body size, number of cells, and number of cell types in different species. They draw pictures of the algae, discuss how different types of cells specialize on different tasks, and talk about how the cells in a multicellular organism work together to allow the organism to survive and reproduce. They observe that a rotifer predator can eat the unicellular organisms but can’t eat the larger multicellular ones. They connect the advantage of living in a group to their understanding of individuals as being entities that survive and reproduce. They discuss how being made of many cooperating cells provides protection from predation and makes the group more motile and more likely to survive.

Guided discussions of life and individuality

We introduce individuality as a foundational concept in the "what is life" guided discussion common at the beginning of many biology classes. For middle schoolers, we give a deflationary account of individuality, defining an individual as an entity that can survive and reproduce by itself. This definition of an individual is the framework for the remaining units. This allows students to become familiar with the core concept of individuality as survival and reproduction (capacity to undergo natural selection) and be more readily able to connect the diversity of life to their understanding of selection and evolution. When encountering new biological units during the year, such as bacteria, organelles, cells in multicellular organisms, parts of a plant, etc., students first ask if it is an individual, focusing on whether the entity can survive and reproduce its characteristics by itself.

Our proposed middle school teaching intervention does not include instruction on the mechanisms by which groups of individuals evolve into a new kind of individual. Relevant topics such as kin selection, conflict mediation, multi-level selection, and reciprocation may be added to the learning progression in high school to develop a more concrete understanding of the mechanistic basis of ETIs. In middle school, concerning individuality, we recommend focusing predominantly on the idea that there are different kinds of individuals that survive and reproduce, and so there are different kinds of groups that may evolve cooperation among their members.

Tree thinking

Although trees are used in middle school, instruction typically does not focus on understanding the causes of a particular tree structure (Catley & Novick, 2008). Including some rudimentary aspects of tree building for the four species introduced in Figure 2 help students understand the timeline of an ETI as well as the characteristics of predicted common ancestors (the nodes in the tree). Using guided discussion and a few traits related to multicellularity (e.g., cells in a group or not, specialized and unspecialized cells) students can build possible trees connecting the four species. Changes in the traits placed along the branches of these possible trees indicate different hypotheses about the intermediate ancestors indicated by the nodes in the tree and these predicted nodes may be compared to the different stages of an ETI. Parsimony may be used to pick among the trees.

Example 2: University Level

Overview of university-level evolutionary biology

In teaching evolutionary biology at the University of Arizona to approximately 180 students in an active learning classroom, we have implemented the same five general tools discussed previously to teach about individuality, cooperation, and the hierarchy of life. Students learn about ETIs through a series of mini-lectures interspersed with table-based activities all guided by a clicker response system.

Analogies of ETIs and student social groups

Students learn about cooperation through a mix of lectures and activities at their tables. Table dynamics serve as an analogy for social dynamics and can leverage their intuitive understanding of social interaction to gain insight into the evolution of cooperation. We ask students to think about what changes when working on a project alone versus working in a group. We ask them to answer a thought question, such as what is life. We first ask students to answer this question alone, not discussing it with their table group, and then ask students to discuss the question with the other students at their table and come up with an answer together as a group. We then convene the whole class and compare the set of individual answers with the group answers. Students typically see that the group answers were more comprehensive than the answers they came up with on their own. We also play cooperation games such as the Prisoner's Dilemma Game that is used in research into the evolution of cooperation. The usefulness of this game for teaching ETIs is based on an analogy between human groups and ETIs.

Cooperation games

Students learn about the mechanisms of the evolution of cooperation, with multi-level selection, kin selection, and reciprocation being taught in some detail during lecture and guided worksheets and study guides driven by clicker response questions.

They play different versions of the Prisoner's Dilemma Game to help them understand why the evolution of cooperation has been considered an important challenge for evolutionary biology. They use clickers to play a single round prisoner's dilemma game according to the following rules. . If they all cooperate, they will all get 5 extra credit points on the final, but if 1 person chooses to defect, that student gets 25 extra credit points and nobody else gets extra credit. Inevitably, multiple students choose to defect, and students see how difficult it can be for cooperation to arise given the benefits of defecting. Students go on to play more involved forms of the Prisoner's Dilemma Game in their discussion sections, where they learn about the tit-for-tat strategy and the evolution of cooperation in scenarios with repeated interactions.

Volvocine algae as a model system

While learning about individuality, the deflationary account of individuality used in lower grades (an individual survives and reproduces on its own) is expanded upon and embedded in Darwin's general postulates of heritable variation in fitness. Students read a paper (Hanschen, Davison, Grochau-Wright, & Michod, 2017) about how to identify and characterize an evolutionary individual using a range of criteria. The volvocine green algae are a case study in this paper, and students examine the algae under the microscope and identify characteristics that affect individuality and the level of selection. Students then break into groups, and each group is assigned an entity that is a candidate for being a biological individual. These entities include single prokaryotic cells, eukaryotic cells, differentiated multicellular organisms, undifferentiated colonial organisms, social groups of primates, and eusocial insect societies. The groups identify which criteria their proposed individual meets, which criteria it doesn't meet, determine what the lower levels and group levels are, and then decide which level they think selection primarily acts at. They then present their results to the class.

Guided discussions of life and individuality

We use clicker response devices to have guided discussions about individuality and life in a large 180-student classroom. The guided discussions involve (i) the difference between individuality transitions and other major events and transitions during the history of life on earth, such as the transition to life on land, or major extinction events, (ii) the role of division of labor and particularly somatic specialization in the evolution of individuality, (iii) what is the genetic basis for ETIs (where do the genes come from), (iv) is individuality a binary trait or does it evolve continuously like most traits, and can there be reversions in individuality, (v) how does heritability in fitness arise at the new group-level when initially it was present primarily at the individual level, and (vi) can individuality be selected for in the lab.

Tree thinking

An activity integrates tree-building and tree-thinking with understanding how ETIs give rise to the hierarchy of life during the origin of the eukaryotic cell (this activity is based on an activity developed by A. Martin at U. Colorado Boulder). Students build phylogenetic trees of the different genomes present in the eukaryotic cell, along with the genomes of archaea, cyanobacteria, and other bacteria. They start with a simple tree containing just bacteria and archaea. They are then asked to draw the tree after an archaea species engulfs a bacterial species (to make a proto-mitochondrion). Then a second endosymbiotic event is considered (to make a proto-chloroplast) and so on. Drawing the trees of all the genomes with the engulfed cells present in the host becomes progressively more difficult. They are then asked to take the endosymbionts out of their hosts and draw the tree of life. This drawing exercise allows them to see how distinct lineages came together to give rise to the eukaryotic cell, a major evolutionary transition in individuality.

Discussion

Overview of science education and our framework for teaching complexity

Our work aligns with broader science education reform initiatives that have been ongoing in the United States for decades (Schmidt, Burroughs, & Cogan, 2013). Continued quests to advance STEM education have been motivated by national and international comparisons that have painted a poor picture of students' STEM competencies in the United States (National Assessment of Educational Progress (NAEP), 2015; National Science and Technology Committee (NSTC), 2018; OECD, 2018). Reform is also advancing within specific domains of science at the university level. For example, within biology education, scholars have increasingly advocated for educational approaches that help students better understand biology, and the nature of science (AAAS, 2011; Dunk et al., 2019). Importantly, reform efforts are not focused solely in the U.S. Recently the *Journal of Microbiology and Biology Education* (*JMBE*), produced a themed series that explored STEM education trends, practices, challenges, and progress on the international front (Karikari et al., 2019).

In the spirit of these efforts, our framework aims to advance biology education by teaching biological complexity. Failure to understand biological complexity has led to negative effects on the public's understanding of and engagement with evolutionary biology. We propose teaching biological complexity by teaching about the remarkable evolutionary transitions in individuality (ETI theory) that have occurred on our planet and bestowed upon life its hierarchical structure.

Our translation of ETI theory into pedagogic content and practice involves (i) new content that must be taught, (ii) teaching tools to teach this new content, and (iii) connecting the new content and teaching tools with the local education context. To illustrate how the framework can be tailored to specific local educational contexts, we provide examples of how we have translated research on ETI theory into the teaching biological complexity in middle school and university-level biology in the United States. However, our framework is applicable to educational contexts outside of the U.S.; in part, because the U.S. system was benchmarked off international teaching practices and standards, but mainly because our teaching tools are general and flexible. They may be tailored and adapted to various student groups and educational contexts.

Bridging ETI theory and the teaching of biological complexity requires the addition of content in three topical areas: (1) individuality as a core concept in biology, (2) cooperation and natural selection in social groups, and (3) the nested hierarchical organization of biodiversity. The logic connecting these three content areas based on research on evolutionary transitions is that the evolution of cooperation in social groups (topic 2) may lead to such a high degree of integration in a group that the group evolves into a new kind of individual (topic 1). This process has happened multiple times during the history of life to produce the nested hierarchy of life we see today (topic 3). Evolutionary transitions research provides a way to teach biological complexity that is familiar and engaging to students, leveraging their inherent understanding of social dynamics and group behavior.

The individual is the biological unit that survives and reproduces, and populations of individuals undergo natural selection. Different kinds of individuals make up the hierarchy of life and these new kinds of individuals have evolved from groups of previously existing individuals. The inclusion of the topic of individuality allows students to think about the importance of survival and reproduction to the diversity of life, which should help them connect disparate elements of their biology curriculum to evolutionary biology. By using individuality as the core concept, and through studying ETIs, students may see the connections between natural selection, genetic drift, biological diversity, and biological complexity.

Relation of teaching ETIs to science practices

In Table 1, we relate the new content (column 1) and teaching tools (column 2) to the teaching of science practices at the middle school (column 3) and university levels (column 4). For concreteness concerning 'science practices,' for middle school we have used the NGSS science practices (NGSS Lead States, 2013), and, for university-level biology we have used the core competencies from Vision and Change (AAAS, 2011, p. page 17). Recall the United States NGSS standards were benchmarked from international standards. These standards are offered as concrete examples of science practices, however, 'science practices' are clearly not specific to any educational system, set of standards, or country. Delineating science practices is a way of describing the process of science. The information about science practices given in columns 3 and 4 of Table 1 was extracted from the activities described above for the two illustrative examples (middle school and university) for the different teaching tools (column 2) and new content areas (column 1).

Table 1. Relation of teaching ETIs to the science practices commonly taught in schools. The NGSS science practices are 1. Asking questions, 2. Developing and using models, 3. Planning and carrying out investigations, 4. Analyzing and interpreting data, 5. Using mathematics and computational thinking, 6. Constructing explanations, 7. Engaging in argument from evidence, and 8. Obtaining, evaluating, and communicating information. The Vision and change core competencies for university level biology are (AAAS, 2011, p. page 17): A. Ability to apply the process of science, B. Ability to use quantitative reasoning, C. Ability to use modeling and simulation, D. Ability to tap into the interdisciplinary nature of science, E. Ability to communicate and collaborate with other disciplines, and F. Ability to understand the relationship between science and society. Practices and competencies in the table are abbreviated; enumeration in table follows the enumeration given in this table legend.

Content areas	Teaching tools	Science practices for middle school	Core competencies for university
Individuality	Question-guided discussion Classroom as an analogy for ETIs Volvocine algae	1. Asking questions 2. Using Models 7. Argument from evidence 8. Communicating information	A. Process of science C. Modeling E. Communication
Cooperation	Game playing Classroom as an analogy for ETIs	2. Using models 3. Carrying out investigations 4. Interpreting data 6. Constructing explanations	A. Process of science B. Quantitative reasoning C. Modeling E. Communication F. Science and society
Hierarchy of life	Volvocine algae Tree thinking	2. Using models 3. Carrying out investigations 4. Interpreting data 5. Computational thinking 6. Constructing explanations	A. Process of science D. Interdisciplinary nature

At the university level, most of the core competencies given in the last column of Table 1 from Vision and Change (AAAS, 2011) concern the process of science, and are relatively straightforward in terms of connecting them to the teaching tools of ETIs as implemented in the classroom described above. However, ETIs have a special connection to core competencies *D.* and *F.* The core competency of *F. Ability to understand the relationship between science and society* has a special interpretation in the case of ETIs, because, as described above, human social dynamics and change map on the stages of an evolutionary transition. In other words, in addition to the many issues involving science and society, in the case of ETIs, there is a literal connection between the study of human societies and the science of ETIs because both are groups of social agents. Concerning the core competency of *D. Ability to tap into the interdisciplinary nature of science*, there is a special connection with ETI content, because the new content area of the hierarchy of life is itself a system of interconnections between different disciplines from molecules to genomes to cells to groups to communities and ecosystems.

Additional aspects of complexity and the hierarchy of life

Although the hierarchical organization of biological diversity is a fundamental aspect of biological complexity, there are other aspects of biological complexity than hierarchical organization and there are other approaches to understanding complexity than through the study of ETIs. For example, there is an entire field of science and computer science called 'complexity science' that seeks to study common features of complex systems. Jacobson and Wilesky (2006) provide an overview and discussion of complexity science for educators. A hub for complexity science is the Santa Fe Institute with its associated faculty, publications, and outreach (Santa Fe Institute, n.d.).

There are other aspects of biological complexity than hierarchical organization, such as organismal design and the organization of diversity into the relatively distinct groupings termed species (Bernstein, Byerly, Hopf, & Michod, 1985; Bernstein, Byerly, Hopf, Michod, & Vemulapalli, 1983). These aspects of complexity are already topics in the biology classroom. Organismal adaptations are explained by natural selection, and, although adaptation is taught, it is usually not connected to complexity and to the process by which new kinds of organisms originate during ETIs. Organisms tend to be treated as fixed categories, but evolutionary transition research explains the process by which new kinds of organisms have evolved. Just as the origin of different kinds of species is taught through speciation theory, so can the origin of different kinds of organisms be taught through ETI theory.

We have focused on the different kinds of individuals that comprise life's hierarchical structure: genes, cooperative gene networks or genomes, simple cells, complex eukaryotic cells, multicellular organisms, and eusocial societies (Figure 1). As often portrayed in biology textbooks, there are levels in the hierarchy of life that are not evolutionary individuals. For example, tissues, organs, and ecosystems are often portrayed as levels in the hierarchy of life, however, these levels are not evolutionary individuals because they do not survive and reproduce by themselves.

Although increased levels of biological complexity have evolved in certain lineages, unicellular organisms dominate the planet today as they likely always have. Complex organisms co-exist with less complex organisms, so evolution cannot be characterized as a progressive march towards increased complexity. Unicellular bacterial and archaeal organisms evolved 3.5 billion years ago and have continued to flourish throughout the history of life on this planet. Less complex organisms survive and reproduce better under many environmental conditions. Complex animals with which we are most familiar make up a tiny component of earth's biomass, while simple unicellular organisms are a major contributor to the biomass present on earth (Bar-On, Phillips, & Milo, 2018). Numerically, of course, bacteria, archaea, and viruses dominate the planet.

Benefits of teaching complexity and evolutionary transitions research

If we look at the landscape of research on the teaching of evolution and ask what is known and what is not known, what are the open questions, and what are the barriers to student understanding, we see that the teaching of biological complexity is front and center to these questions. It appears from the current literature on evolution content in K-12 (Ziadie & Andrews, 2018, 2019) that not much is known about how to teach biological complexity per se for the topic does not appear in reviews of evolution content knowledge. A barrier to student understanding of evolution is how teachers should teach complexity and an open question is how to include the teaching of complexity in K-12 learning objectives and content. The use of ETI theory to teach the hierarchy of life provides an answer to these questions.

There is some urgency to teach biological complexity because its omission from the science classroom has created a void in student understanding of biological diversity. Although the relationship between acceptance of evolution and understanding evolution is complex (Dunk et al., 2019; Ha, Haury, & Nehm, 2012; Nehm, 2019), we think that not addressing biological complexity head-on has created a misunderstanding in the public that evolution cannot explain the dramatic jumps in complexity that result in the hierarchy of life. This is not only a missed opportunity but has created an opening for non-scientific theories of complexity such as intelligent design (Behe, 2006; Dembski, 2002).

Translating research areas into the classroom is a challenging yet ultimately rewarding practice for teams of researchers and teachers. For us, it involved a three-pronged approach: new content, new teaching tools, and mapping our research area onto the local teaching context and grade level. We identified the teaching of biological complexity per se as a missing topic in the biology classroom. The framework proposed here is just the beginning. Connecting research to educational practice is a long-term endeavor that requires teams of scientists and educators to collaborate to develop new approaches and tools. Further addressing this and other gaps in instruction by teams of researchers and teachers will help move science education forward and address The National Academies' recent "Call to Action for Science Education" (National Academies of Sciences Engineering and Medicine, 2021). Evolutionary biologists have devoted their work to understanding the processes that have led to our amazingly complex and diverse world. Our increasing knowledge about these processes gives us an opportunity to leverage this knowledge to promote the public's deeper understanding of and engagement with complexity in biology.

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