8-23-2024

Defining Evolution: Exploring Students' Conceptions of Evolution in Introductory Biology Courses

Jeremy L. Hsu
Chapman University, hsu@chapman.edu

Meredith A. Dorner
Irvine Valley College

Kate M. Hill
Chapman University

Recommended Citation

Hsu, J.L., Dorner, M.A. & Hill, K.M. Defining evolution: exploring students' conceptions of evolution in introductory biology courses. *Evo Edu Outreach* 17, 14 (2024). https://doi.org/10.1186/s12052-024-00208-x

Hsu *et al. Evolution: Education and Outreach* (2024) 17:14
https://doi.org/10.1186/s12052-024-00208-x

Evolution: Education and Outreach

RESEARCH Open Access

Defining evolution: exploring students' conceptions of evolution in introductory biology courses

Jeremy L. Hsu[1*], Meredith A. Dorner[2] and Kate M. Hill[1]

Abstract

Background Understanding evolution is an important part of undergraduate biology education. Despite its importance, however, students often struggle to understand evolution, often holding preconceived notions of what evolution is. Here, we investigate how students in both majors and non-majors introductory biology define and conceive of evolution at the start of the semester for a two-year college and a four-year university near each other. We analyze open-ended responses to an in-class activity on the first day of the semester that asked students to define evolution, generating insight into how students are thinking of evolution prior to any formal instruction on evolution in college.

Results Our analysis of over 300 student responses reveals that students hold diverse conceptions about evolution, with some students perceiving evolution in the context of evolutionary processes while other students define evolution by referring to perceived evolutionary consequences. In addition, we identify multiple non-normative conceptions about evolution, including students viewing evolution and natural selection as synonymous and not recognizing other evolutionary forces, and find that very few students likely have developed mental models linking evolution and genetics. In addition, we find few differences between how students at the two- and four-year institutions perceive evolution, and similarly few differences between students in a majors and non-majors introductory biology, suggesting that these conceptions of evolution are widespread at the beginning of introductory biology, regardless of major or institution.

Conclusions We situate our results in the existing literature examining student conceptions of evolution, with our results extending past work that has primarily relied on more closed-ended questions or focused on specific evolutionary concepts (e.g., natural selection). Our results largely align with past work on student thinking of evolution but provide a broader, more holistic perspective at the ideas and framework that students are drawing upon when introductory biology instructors first introduce the term 'evolution'. We conclude our paper by discussing implications for the biology education research community as well as instructors.

Keywords Evolution education, Undergraduate, Introductory biology

*Correspondence:
Jeremy L. Hsu
hsu@chapman.edu
[1]Schmid College of Science and Technology, Chapman University, One University Drive, Orange, CA 92866, USA
[2]Irvine Valley College, 5500 Irvine Center Dr, Irvine, CA 92618, USA

Introduction

Teaching evolution is a crucial part of undergraduate biology education, and its importance has been highlighted in multiple national reports. For instance, the 2011 *Vision & Change* report highlighted evolution as one of the five core concepts for undergraduate biology education (American Association for the Advancement of Science, 2011) and a subsequent evolution education convocation held by the National Research Council of the National Academics of Science brought together various stakeholders in biology education to improve evolution education (National Research Council 2012; Wei et al. 2012).

Despite its importance, there remain multiple challenges for teaching evolution in undergraduate biology education. For instance, these include perceived conflicts between religion and evolution leading to potentially low rates of evolution acceptance and perceived utility for learning evolution among some groups of students (Barnes et al. 2020; Borgerding and Kaya 2022; Misheva et al. 2023). In addition, many students and instructors (including in K-12 education) struggle to understand the nature of evolution, often misinterpreting what a scientific theory represents and not recognizing the overwhelming amount of evidence supporting the theory of evolution (Cavallo and McCall 2008; Dagher and Boujaoude 2005; Jensen and Finley 1996; Yates and Marek 2014). There have also been multiple studies examining how students think about evolution, identifying numerous misconceptions about evolutionary processes, phylogenetic trees, and adaptations (Andrews et al. 2012; Furrow and Hsu 2019; Kampourakis 2020; Meir et al. 2007).

These studies have also identified that students entering a college biology classroom likely hold many cognitive biases about evolutionary processes. For instance, one study asking college students prior to any formal learning on evolution to provide explanations for several scenarios featuring evolutionary change driven by selection identified that students were likely to describe natural selection as goal-directed and ascribe evolutionary agency to individual organisms, believing that individual organisms have the ability to "choose" to evolve by changing their behavior and influencing the next generation (Moore et al. 2002; Nehm 2018), with such anthropomorphic and teleological explanations documented in multiple other studies (Barnes et al. 2017; González Galli et al. 2020; Hartelt et al. 2022; Kampourakis 2020; Legare et al. 2013; Stover and Mabry 2007). Other studies have found that similar misconceptions already exist in elementary school students, and that these misconceptions persist in students in secondary and postsecondary education (see summary of papers in Gregory 2009) and even extend to graduate students in the sciences (Gregory and Ellis 2009). Similarly, other work has identified that many preschool age children already hold views of change that are driven by essentialist thinking, a cognitive bias where individuals think of organisms as holding immutable, essential traits that define their identity, making it more challenging to grasp the mechanisms of natural selection (Hartelt et al. 2022; Shtulman and Schulz 2008). Other studies and reviews have identified that students often think of evolutionary change in the context of need/necessity (Bardapurkar 2008; Cavallo and McCall 2008). Another study that examined how undergraduate students thought of evolution on the first day of class in an introduction to biological anthropology course identified that many students hold misconceptions about selection, and that most students also do not comprehend the nature of genetic variation and mutation (Cunningham and Wescott 2009).

However, this past work on understanding student thinking about evolution is limited in several ways. First, most of these studies investigate how students explain biological change, primarily by providing scenarios that illustrate changes driven by natural selection or by providing a series of possible biological explanations for a given scenario and asking students if they agree or disagree with each explanation. These studies offer insight into students' reasoning of biological phenomena and evolutionary mechanisms, but do not explicitly probe how students think of the *concept* of evolution itself (as opposed to students' understanding of specific evolutionary forces potentially responsible for changes). In addition, most of the studies we identified that examined students' conceptions of evolution focused on providing scenarios of change driven by natural selection, with very few studies we are aware of that examined students' conceptions of evolution at large as a biological phenomenon. Similarly, there have been multiple student misconceptions uncovered during the creation of concept inventories about a given evolutionary concept (e.g., natural selection; phylogenetics; genetic drift, etc.); these validated assessments are usually developed through an iterative process that often involves interviewing students to identify how students are conceptualizing a given evolutionary concept (D'Avanzo 2008; Furrow and Hsu 2019). However, these insights into student thinking are usually limited to the specific evolutionary concept covered in the concept inventory, and we are not aware of any work to date that has explicitly asked undergraduate students to characterize evolution, leaving a gap in the literature regarding how students think about the term 'evolution' or what evolution means.

In addition, nearly all of these studies have been conducted in the context of undergraduate students enrolled at research-intensive four-year colleges or universities (i.e., institutions that award students bachelor's degrees), with much more limited evolution education work examining how students at non-research intensive universities or two-year colleges (i.e., institutions that award associate's degrees, including schools that are vocational in nature) think about evolution (Barnes et al. 2022). An analysis of published biology education research literature from 2019 identified that fewer than 1% of sampled work was conducted in the context of two-year colleges, suggesting that there is an urgent need to increase our understanding of how students think and learn biology at two-year colleges (Lo et al. 2019). Indeed, the limited studies that examine how students at two-year colleges think about evolution have revealed that there are likely differences among those students and their peers at four-year colleges. For instance, a study that surveyed students at seven 2-year colleges across multiple states and compared them to students at nine 4-year institutions found that while students at 2-year colleges had roughly comparable levels of interest in learning about evolution, they had on average lower levels of understanding of evolution and lower rates of evolution acceptance than their peers at 4-year institutions (Barnes et al. 2022). Other studies have also found generally low levels of understanding of evolution among students at 2-year colleges (Brown and Scott 2016; M. Dorner 2016; Flower 2006; McKeachie et al. 2002). Similarly, students at 2-year colleges perceived greater conflicts between religion and evolution than their peers at 4-year institutions, with no correlation between understanding of evolution and acceptance of macroevolution or human evolution, in contrast to students at 4-year institutions (Barnes et al. 2022). However, other studies that have explored a more limited number of 2-year colleges have found contrasting results, suggesting that there is likely variation in the level of evolution understanding and acceptance among 2-year colleges in different regions of the United States (Dorner and Scott 2016). In addition, other studies set in the context of 2-year colleges have found differences in students' level of understanding of evolution among courses for biology majors and those for non-majors, suggesting that there is likewise potentially large variation in how different students within 2-year colleges think about evolution (Dorner et al. 2023), and that students in the 2-year college classroom likely hold a diverse set of cultural worldviews that shape their conceptions of evolution (Green and Delgado 2021). These differences are likely driven by the different demographics of students at 2-year colleges than 4-year institutions; for instance, students at 2-year colleges are more diverse than their counterparts at 4-year colleges, with more students from historically marginalized backgrounds and low socioeconomic status and a greater proportion of first-generation students and students who have taken gap years between secondary and postsecondary education (Barnes et al. 2022; Kisker et al 2023). Despite these differences, we are only aware of one other evolution education study that has directly compared student thinking between 2- and 4-year institutions (Barnes et al. 2022), suggesting that there is an urgent need to continue investigating how students at 2-year colleges think about evolution and contrasting these patterns with students at 4-year institutions to identify what factors may be shaping students' understanding and acceptance of evolution.

We thus investigated the following research questions:

1. How do students at the start of introductory biology at a two-year college and a non-research intensive four-year university define evolution? What are the qualitatively different ways that students characterize evolution?
2. Are there differences in how students at a two-year college and four-year university in close geographic proximity define evolution?
3. What differences, if any, are there in students' definitions of evolution in a general biology course for non-science majors as compared to introductory biology courses for science majors?

Conceptual framework

We first situate our study through the lens of constructivism and then utilize thematic analysis for our methods. Constructivism is a learning theory that posits that students construct mental models of meaning where new information is scaffolded to fit within and extend existing mental frameworks of prior knowledge (Bada and Olusegun 2015; Fosnot and Perry 1996; Hodson and Hodson 1998). Thus, how each student learns is heavily dependent on not only the current context of learning and how such information is presented, but also on their past conceptions and ideas relating to a topic, which can influence how they interpret and make meaning of new information (Cakir 2008). In this study, we examined undergraduate students' initial perceptions of evolution using an in-class activity. This allowed us to characterize their conceptions of evolution before any formal instruction on the subject in the course. Our goal was not to determine the impact of instruction on students' thinking about evolution in the course, which would be heavily influenced by the class's specific curriculum and instruction, but instead to capture the range of conceptions of evolution that undergraduates have entering the course, which may shape how students learn and think about evolution.

In addition, our goal was not to measure student understanding of evolution (which would require us to utilize validated instruments that probe student thinking of different aspects of evolution), nor was it to capture students' explanations for biological change, which students may or may not associate with the concept of evolution. Instead, our goal was to determine how students are characterizing and defining the term 'evolution' and the biological concept that this term represents at the beginning of the semester, providing insight into what ideas students are bringing into the undergraduate classroom when the instructor mentions the term 'evolution'. Our work builds upon other studies that have asked students to define a given term in order to characterize students' perceptions of a given scientific concept or process (Arizaga et al. 2016; Van Rossum et al. 1985). Given that many instructors of introductory biology begin a module on evolution by first defining what evolution is, our aim was to generate new insight into what students think evolution is when the instructor first mentions the term prior to any formal learning about evolution in college. Thus, our work is distinguished from past studies by challenging students to explicitly define evolution in an open-ended way, rather than relying on scenarios that illustrate specific evolutionary mechanisms (usually natural selection) or specific Likert-scale questions that probe how students think about evolutionary mechanisms and variation.

We also focus on introductory biology given that this is likely the first biology course taken by biology majors in college (and the first biology course for non-STEM majors taking non-majors introductory biology), and that evolution has been identified as a core concept that should be taught nearly ubiquitously across introductory biology courses (Brownell et al. 2014). Despite its importance, however, many students in high school and college still struggle to comprehend evolution, and understanding the ways that students are thinking about evolution upon entering introductory biology can facilitate the development of curricular interventions that can promote deep conceptual understanding of evolution and counter misconceptions (Alters and Nelson 2002).

Finally, we utilize thematic analysis, drawing upon both inductive and deductive coding for our methodology. This approach allows us to identify themes that emerge from the data, while also drawing upon our knowledge of theory and past evolution education work to inform our codes. Thus, our approaches centered on iteratively reviewing, analyzing, and discussing the themes that emerged from students' qualitative responses to the in-class question (see methods section below) with the goal of identifying emergent themes in how students are defining and characterizing evolution. Finally, we place the emergent themes in students' perspectives of evolution within the context of existing literature on evolution education.

Methods

Institutional and course context

This study was conducted at two Southern California institutions in close geographical proximity to each other, allowing for a comparison of student conceptions of evolution between these institutions given that past work has identified that students' understanding and acceptance of evolution may vary by geographic region (Barnes et al. 2022; Kelly et al. 2016). The first is a private, comprehensive university without any biology graduate programs. The second is a two-year college that only grants associate degrees. Both institutions have a two-semester introductory biology sequence, oftentimes split into multiple sections each semester with enrollment between 20 and 70 students per section, taken predominantly by science majors. While most students take introductory biology I prior to introductory biology II, students can take the courses in either order since introductory biology I is not a prerequisite for introductory biology II at either institution. Thus, to capture the broadest range of student conceptions, we included students in both introductory biology I and introductory biology II in our analyses. In addition, the two-year college also offers a general biology course targeted for non-science majors; we also included students in this course to compare how students in majors and non-majors introductory biology define evolution.

First day of class activity

For our study, we utilized a fortuitous data set that was collected from an activity that was deployed on the first day of the semester in spring 2022 and fall 2023 across multiple introductory biology classes. In this activity, students were first asked "what is evolution?" Students were given time to think individually to themselves and then were asked to write down their responses on an anonymous online form, prior to being asked to discuss their responses in small groups. The activity was typically completed within five minutes, with instructors asked to provide sufficient time for students to finish writing their responses prior to discussing the results. This activity has been used by the authors in multiple past introductory biology and evolution courses on the first day of class to elicit how students are thinking of and defining evolution; the question is deliberately open-ended to allow the instructors to characterize the variation in how students view and define evolution in a given class, with the resulting answers used to inform pedagogical choices when defining and discussing evolution with the class. The timing of this activity thus ensures that student responses reflect student views of evolution prior to instruction in that semester's introductory biology course and facilitates a high response rate given that this activity was done in class. We gathered a total of 326 responses

Table 1 Overview of courses included in the study across two institutions. *The number of students enrolled in the class represents the official enrollment for the course, which is taken after the institution's add/drop period the first two weeks of the term. The activity was given to students on the first day of class. Thus, there may be a greater number of students present for the first day of class than still enrolled after the end of the add/drop period. Similarly, it is possible that some students added after the first day of class. Response rates are calculated from enrollment data

		Institution 1 (four-year university)	Institution 2 (two-year college)
Introductory biology I	Number of sections	1	2
	Number of responses (enrollment; response rate)	60 (61 enrolled; 98.4% response rate)	36 (70 enrolled; 51.4% response rate)
Introductory biology II	Number of sections	1	3
	Number of responses (enrollment; response rate)	55 (58 enrolled; 94.8% response rate)	83 (99 enrolled; 83.8% response rate)
Non-majors general biology	Number of sections	Not offered	2
	Number of responses (enrollment; response rate)	Not offered	93 (88 enrolled; 105.6% response rate*)
Total	Number of students	115 (119 enrolled; 96.6% response rate)	211 (257 enrolled; 82.1% response rate)

(86.7% response rate) across both institutions (Table 1). The procedure was reviewed and approved by both institutions' Institutional Review Boards.

Analysis

Each author first read 36 responses (representing over 10% of the total number of responses and drawn to ensure equal representation from each course across institutions) and independently generated codebooks following the principles of thematic analysis (Braun and Clarke 2012; Peel 2020). Next, the authors met to discuss and come up with a consensus codebook (Table 2). During this discussion, we drew upon our own experiences and expertise with evolution and evolution education during these discussions, as well as our knowledge of the evolution education literature. For instance, all three authors are current biology faculty who hold Ph.D.s in ecology and evolutionary biology (JLH, KH) or evolution education (MD) and regularly teach evolution courses. The authors have published extensively both in evolution and ecology (Hsu et al. 2017a, b; Solari et al. 2016; Zhan et al. 2014) as well as evolution education (Dorner et al. 2023; Dorner and Scott 2016; Forsythe and Hsu 2023; Furrow and Hsu 2019; Hsu et al. 2021; Hsu 2020), and our discussions drew upon this literature and our own experiences, supporting the validity of our codebook.

Following this, the authors collaboratively coded the 36 responses, discussing each response and code to ensure reliability. Each response could be coded with zero, one, or more than one code, depending on what theme(s) the student conveyed in their response. Next, each author independently read and coded another random 36 responses, which were again drawn to ensure equal representation across courses. We calculated Fleiss's kappa using ReCal3 (Freelon 2013), checking interrater reliability for each code applied per quote. Kappa was 0.759, indicating "substantial" agreement between coders (Landis and Koch 1977). Given this high interrater reliability, each author coded one-third of the remaining responses. To further ensure reliability, each coder flagged any responses they were unsure about and the three authors collaboratively discussed and coded this small subset of responses that were flagged at the end.

We compared the frequency of codes across courses and institutions with Pearson's chi-squared tests with *post-hoc* Bonferroni corrections to account for the multiple comparisons being done (one comparison per code). In addition, we also identified the number of co-occurrences of each code and found the percent of each code co-occurrence among total responses. In addition, after finishing coding, the authors met to discuss each of the codes and identify any larger, axial themes emerging from the data, and situate these themes in the broader evolution education literature. Iterative discussion among the authors then informed the creation of a model that incorporates all 11 codes, providing a perspective on how students think about what evolution is.

Results

Students hold a wide range of conceptions about evolution

Students provided a diversity of definitions for evolution, ranging from characterizing evolutionary processes to describing perceived consequences of evolution, like the formation of new species (Table 2). There was no consensus among students on what evolution is; the most common theme (conveyed by 56.7% of respondents) was that evolution involved change (Table 2). Responses in this category were explicit about defining evolution as a process involving change, and responses ranged from students incorrectly viewing evolution as the change of an individual organism (e.g., "Evolution refers to the process where a living organism adapts and modifies its body to become better suited to survive in its environment") to students correctly characterizing evolution as a change in a population over time (e.g., "It describes the changes in genetic traits in a population over a time period including natural selection and the favoring of traits that allows the organism to better survive in the specific environment.").

Table 2 List of codes for how students responded to the question of "What is evolution?" Only codes with 5% frequency or greater were included in our analyses, excepting the code of 'descent with modification', which we include despite its low frequency given the usage of this phrase by Charles Darwin and its usage in common parlance as a term for evolution

Code name	Code definition	Sample quote	Percent of responses
Change	Associates evolution with change, including organisms changing over time	"Evolution is the change in organisms over times between generations" "A change in a characteristic of a species over time" "Change over time"	56.7%
Natural selection	Characterizes evolution as different traits being favored by the environment, i.e., defines evolution through the lens of adaptation or selection	"Organisms changing over time to adapt to their current environment." "Noticeable changes and characteristics throughout time to adapt" "Evolution is the process of a species/organisms adapting to new environments."	53.1%
Agency/ intentionality	Implies that evolution consists of organisms choosing or needing to change (i.e., making conscious choices that influence their evolution), either at the individual or population level	"Evolution is the process by which an organism changes itself over time as it adapts to changes in its surroundings." "The ability of an organism to make genetic changes over long periods of time in order to adapt and survive in changing environments." "Evolution… can be explained as adaptations made by the living creature in order to survive. The purpose of evolution is for the living creature to thrive in its every changing environment."	23.6%
Survival	Defines evolution through the lens of organisms surviving environmental and ecological changes; includes responses with the phrase 'survival of the fittest'	"Evolution is the way in which organisms have adapted to their surroundings over time, and the way they have been able to survive changes in their environments." "Evolution is the gradual change in a species across a large timespan which should facilitate successful survival of member organisms." "Evolution is the process that all organisms do to survive. It is done through many types of adaptations and happens so that organisms can survive."	22.4%
Progress	Defines evolution as a progression through time, with an implied or explicit statement of progress from simple to complex or primitive to advanced; this includes if student associates evolution with advancement or progression, i.e., viewed evolution in a forward-thinking manner	"Evolution is the progressive development of living organisms through time base on their ability to adapt to their ever-changing environment." "The gradual development of something, especially from a simple to a more complex form." "Evolution is the process of organisms progressing from mRNA to more and more complex organisms over time. During this process, species evolve as a result of different pressures."	22.4%
Gradualness	Discusses evolution as a slow process, or one that takes place over a long period of time	"I would define evolution as the processes of change that occur to living organisms & species over a gradual period of time." "The process of slow change in species based on genetic mutations generationally according to the natural selection of optimal traits based on the species members' biome, other relevant wildlife and other environmental factors such as climate." "Evolution is when natural selection takes place and a population slowly begins to develop or lose characteristics to make them more fit for survival"	17.5%
Genetic variation	Discusses differences in DNA or genes within a population, or genetic changes (e.g., mutations)	"Evolution is the changing of genes over a period of time." "That is to say, under the influence of factors such as natural selection and genetic variation, species will gradually change their characteristics to adapt to the environment." "Evolution is the process by which living organisms gradually change over time through the accumulation of genetic changes in their populations."	14.1%
Change within an individual	Describes evolution in the context of an individual changing, i.e., changes in an individual over the course of that individual's lifetime	"Evolution refers to the process where a living organism adapts and modifies its body to become better suited to survive in its environment." "From what I understand, evolution is a process by which a living organism changes their behavior or anatomy to better suit their environment over time." "The development of new traits/characteristics over an organism's lifetime. This can happen naturally or in order to adapt to a change in environment or other types of changes"	12.6%

Table 2 (continued)

Code name	Code definition	Sample quote	Percent of responses
Varying units of evolution	Indicates that evolution can occur across multiple levels of organization, such as genes and individual species	"The development of genes, humans, and animals through long periods of time." "Evolution is the change of something over time for example it could be a change of a specific characteristic or an entire species" "Microevolution comes about through mutations such as blue eyes or small alterations in beak size. Macroevolutions comes about through punctuated evolution which can be observed in the fossil record"	5.8%
Speciation	References evolution as a process by which new species can form	"It is a theory that explains how a new species variety comes from previous adaptations from new adaptations and natural selection" "Evolution is an extensive and slow process that occurs over thousands of years. This process is driven by natural selection and the environment which leads to the alteration and divergence of species." "Evolution is the natural engine of organic research and development on Earth. It is a collection of processes and events that give rise to new species over time"	5.5%
Descent with modification	Explicitly uses the phrase "descent with modification" in their definition	"I like to think of the phrase 'descent with modification', and over time as generations of species carry out they may experience adaptations, physical changes, or in general differences from the generation prior to them." "Descent with modification"	1.2%

The only other theme conveyed by most students (53.1% of respondents) defined evolution as natural selection, which included responses that conveyed ideas of adaptations and differential fitness in a population. All responses that invoked themes from selection, adaptation, or differential fitness were included in this code, regardless of the level of detail presented. For instance, one student wrote a short definition that evolution is "the process in which organisms adapt to their surroundings," while another student wrote that "evolution is a result of the survival of the best fit. Species change gradually over time in response to their environment, which means that new traits can become more common in a population while others might become less common or even disappear. This happens because individuals with traits that help them survive and have more babies tend to pass those helpful traits on to their offspring." These quotes, though providing varying levels of detail that reflect potentially different understandings of natural selection, convey that each student is viewing and defining evolution through the lens of natural selection.

Intriguingly, selection was virtually the only evolutionary mechanism cited by students. No students mentioned random genetic drift, gene flow/migration, or recombination, and very few students (3.7%) cited mutation in their definition of evolution. We note, though, that these mechanisms (along with selection) can impact genetic variation in a population. However, fewer than 15% of students included any indication of genetic variation or genetic change in their responses, and only 20 students (6.1% of respondents) defined evolution through the lens of both selection and genetic variation in their response. For example, one student wrote that evolution is "the ability of an organism to make genetic changes over long periods of time in order to adapt and survive in changing environments." While this response provides some inaccuracies in their conceptions of evolution (which are discussed in the paragraphs below), the student puts forward a conceptual connection between adaptation and genetic change, which few students explicitly connect in their responses.

The third most common code was students implying that evolution was a process where individual organisms or species could choose to evolve certain traits or to adapt in response to ecological changes, a theme conveyed by approximately a fourth of students (Table 2). This code aligns with past literature that has found that many students hold non-normative ideas where individuals or species can have "intentionality" in making conscious choices that would impact their evolution (Nehm 2018). In these responses, students hinted at individual organisms, populations, or species having the agency to evolve, rather than viewing evolution as a process or mechanism for change in a population and placed individual organisms or species as the main actor of evolution. Indeed, in the previous quote ("the ability of an organism to make genetic changes over long periods of time in order to adapt and survive in changing environments"), the student explicitly defined evolution as an organism's ability to change itself and its genetic makeup in order to adapt to changing environmental conditions, suggesting that individual organisms have a choice or agency in evolution.

A little over a fifth of respondents (22.4%) defined evolution through the lens of organisms surviving environmental and ecological changes over time. Many students who defined evolution by citing survival of different individuals also highlighted natural selection; these codes co-occurred in nearly all (82.2%) students' responses who characterized evolution as survival of different organisms or individuals, likely reflecting many students correctly viewing selection as being driven by differential survival of individuals in a population. “Evolution is the way in which organisms have adapted to their surroundings over time, and the way they have been able to survive changes in their environments,” one student wrote, illustrating that they are conceptualizing how adaptations may lead to greater survival.

Approximately another fourth of students (22.4%) presented a view of progression or advancement when defining evolution. These students view evolution as organisms getting ‘better’ or eventually reaching ‘perfection’, often citing how evolution causes organisms to change from simple to complex, primitive to advanced, or from ‘bad’ to ‘good’. “Evolution is the idea or concept of an entity or species progressing forward, adapting, and or evolving into something better and or more practical for whichever situation they may encounter,” one student wrote.

Three codes were found in between 10 and 20% of responses. Nearly a fifth of students (17.5%) conveyed that they viewed evolution as a gradual process or one that takes a long period of time. Nearly 15% cited genetic variation, and approximately an eighth of students (12.6%) defined evolution by citing changes in individual organisms rather than changes in a population (Table 2). “Evolution refers to the process where a living organism adapts and modifies its body to become better suited to survive in its environment,” one student wrote, implying that they view evolution as a singular individual altering its traits to better survive. We identified that this code had high levels of overlap with both the “agency/intentionality” and “change” codes (supplemental Table 1). However, this was marked as a separate code since some students discussed the non-normative idea of how evolution involved an entire population or species choosing to evolve, thus fitting with the “agency/intentionality” code but not within the “change within individual” code. Similarly, it was possible for students to mention evolution as change but without referring to the non-normative idea of specific individuals altering their behavior or genetics that would then drive change.

Approximately 5% of students defined evolution as leading to the formation of new species (5.5%) or cited how evolution involved change at different scales or levels of organization (5.8%) (Table 2). For instance, several students explicitly cited how evolution involved changes at both the genotypic and phenotypic level, while others defined evolution at both a micro- and macro-evolutionary perspective. “Microevolution comes about through mutations such as blue eyes or small alterations in beak size,” one student wrote. “Macroevolutions comes about through punctuated evolution which can be observed in the fossil record, most notably between the Cambrian and pre-Cambrian eras. The process by which it occurs is unknown.” These responses are united through defining evolution through at least two different scales or levels of organizations, even if the student did not conceptually connect the changes in these two.

Only 1% of students defined evolution with the phrase “descent with modification” (Table 2). We included this code, despite its low frequency, given its historical significance as a phrase Charles Darwin used and the fact that many students may have heard this phrase before due to its historical significance (Penny 2011).

Finally, we identified how frequently each unique pair of codes co-occurred within the responses (supplemental Table 1). The codes natural selection and change were the most frequently co-occurring codes (25.5% of responses), followed by natural selection and agency/intentionality (20.9%) and natural selection and survival (18.4%). No other pair of codes occurred in more than 15% of responses.

These student conceptions about evolution can be grouped into four broader categories

We identified that these 11 codes can be grouped into four broader, axial categories (Fig. 1). First, several of the codes (change, natural selection, agency/intentionality, survival, and genetic variation) reveal that these students may be thinking of evolution as a process and are providing responses that provide some insight into how these students are conceptualizing evolutionary processes. In contrast, other students provide responses that instead suggest that they are thinking of the consequences of evolution (e.g., evolution leading to progress or causing new species to form). Other students provided responses that conveyed their perceived attributes of evolutionary change (e.g., students highlighting that evolution is slow and gradual), while others hinted at recognizing some unit of evolution (e.g., those that thought that evolution acted on individuals and that individuals evolve, etc.).

However, we highlight how our grouping of codes into these broader themes is not meant to be exhaustive, and that many of these codes can span across more than one of these themes. For example, students may discuss evolution in the context of selection causing an increase in the frequency of certain adaptations, which would indicate that the student is thinking about evolution both as a process (natural selection) and about the consequences of that process (the adaptations and their change in frequency). Similarly, several words related to evolution may have lexical ambiguity, thus making it challenging to infer the true meaning of student responses (Rector et al. 2013). Thus, each code may fall under more than one theme, but we placed each code with the theme it most aligned with based on the student responses to form an exploratory framework for how students may be thinking

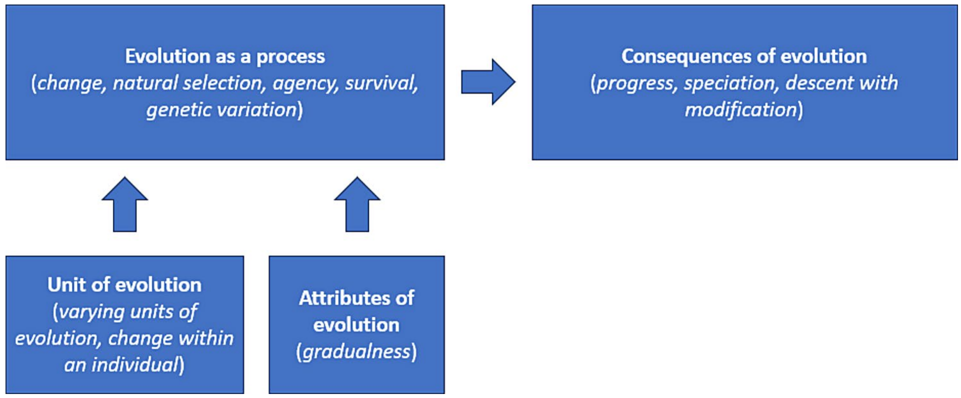

Fig. 1 Different student conceptions of evolution. Each code is shown in italics with the theme it most closely falls under based on the student responses, though each code can span more than one theme. We have used arrows to denote how some of these broader axial themes relate to each other. For instance, students' thinking about the attributes and units of evolution can impact how they think of evolution as a process. Similarly, how students think about evolution as a process will likely influence how they think about the consequences of evolution

of evolution when responding to our prompt. We also highlight how there is a range of variation within each code. Some responses may contain normative (scientifically correct) ideas while others may contain non-normative (naïve) ideas, which have been found to common in student thinking (Gregory 2009; Nehm 2018). Similarly, responses from one student may contain both normative and non-normative ideas. We include a brief discussion of common normative and non-normative ideas for our codes in the discussion. Given these limitations, we caution against overinterpretation of our model and instead highlight how we view our model as a putative way to organize the different codes and responses that students provided to the prompt of "what is evolution?", providing a framework for us to discuss the broader themes and situate our results in the broader evolution education literature.

No differences in how students view evolution between institutions and few differences between classes at institutions

We found no differences in how students defined evolution between the two institutions (supplemental Table 2), including when comparing introductory biology 1 courses among the two institutions (supplemental Table 3). There was only one difference when comparing introductory biology 2 courses across the two institutions, with a larger percentage of students at institution 1 indicating that they defined evolution through the lens of natural selection (67.3–38.6%; supplemental Table 4).

For institution 1 (the four-year university), we only found two differences in how students defined evolution between introductory biology 1 and introductory biology 2 (supplemental Table 5): first, a greater proportion of students highlighted genetic variation in introductory biology 2 (3.3% in introductory biology 1 and 21.8% in introductory biology 2). Similarly, a greater percentage of students defined evolution through the lens of survival in introductory biology 2 (40.0%) than introductory biology 1 (8.3%). In contrast, there were no differences in how students defined evolution in the two introductory biology courses at institution 2 (supplemental Table 6). Finally, students in the general biology course for non-STEM majors at institution 2 largely defined evolution similarly as the students enrolled in the introductory biology courses for STEM majors at that same institution (supplemental Table 7). The only exception was that a larger percentage of students in the general biology course for non-majors defined evolution through the lens of natural selection (64.5%) than students in the introductory biology courses for majors (42.0%, supplemental Table 7).

Discussion

Our results provide insight into how students conceptualize and think of the concept of evolution upon entering introductory biology at two institutions. We found no consensus on how students defined evolution, instead uncovering a wide variety of ways in which students described evolution. Indeed, our 11 codes can be further grouped into several broader themes that describe how students are defining evolution (Fig. 1). First, we see that most students described evolution as a process, i.e., define evolution through the lens of an evolutionary mechanism (e.g., natural selection) or the process of change itself. There were also multiple non-normative conceptions of evolution as a process, including students who attributed evolutionary processes to a perceived 'need' for organisms to evolve. At the same time, many students also highlighted perceived consequences of evolution, e.g., mentioning how evolution leads to progression of a species or the formation of new species. Interestingly, these different conceptions of evolution are similar in nature to how the word 'mutation' has been found to be confusing to students due to its different meanings (i.e., the process of a mutation occurring versus the resulting mutation itself) that cause students to have different conceptions of what a 'mutation' is (Zhao and Schuchardt 2019). Finally, we see that other students described either perceived attributes of evolution (i.e., its perceived slowness as a process) or demonstrated their understanding (or lack thereof) of the unit of evolutionary change. For instance, some students (incorrectly) conveyed how they viewed evolution as changes within an individual, indicating that they were conceptualizing evolution at the scale of individuals changing, while other students were able to connect evolution to multiple levels of change (e.g., recognizing that a mutation within an individual could contribute to genetic variation within a population).

Students view evolution as change, but often incorrectly conceptualize the process of change

Most students viewed evolution as a process, with the two most common codes (change and natural selection) aligning most directly with this theme. Perhaps unsurprisingly, many students defined evolution as a process of change, aligning with past work that has found that even novice learners of evolution associate evolution with change (Andrews et al. 2012; Nehm and Ridgway 2011). In addition, we identified that some students have normative conceptions of evolution as change that suggest they are beginning to form scientifically accurate conceptions of evolution. For example, one student wrote that "evolution is the change in organisms over times between generations," suggesting that they recognized that evolution is not a process of individuals changing, but of changes in a population over generations. Another student wrote that "evolution is a process of change or adaptation typically for the better. In terms of biology it would refer to the gradual series of adaptations a species undergoes as a result of random mutations; mutations that are beneficial usually survive and increase throughout the gene pool until it becomes characteristic of the population." Here, this student – while defining evolution as driven by natural selection and using some imprecise language– provides a largely correct explanation of selection that recognizes genetic variation created by mutations and the likely increase in frequency of beneficial mutations due to natural selection.

However, our results indicate that many students are constructing mental models of evolution based on incorrect, non-normative conceptions of evolutionary change as a process, and are not correctly recognizing at what level evolution acts on. For instance, over an eighth of students viewed evolution as driven by changes in an individual, rather than changes in a population. "Evolution is a process by which a living organism changes their behavior or anatomy to better suit their environment over time," one student wrote. Their response indicates that they are viewing evolution as a process where an individual organism can alter its behavior or traits and pass along those changes to their offspring genetically, signaling that they are building a model of evolution based upon changes in individuals rather than the correct definition of evolution as a process of change in allelic frequencies in a population (Herron and Freeman 2007). Similarly, this student's response demonstrates that they are building an incorrect model of evolution where organisms have agency to evolve, i.e., making a conscious, intentional decision that then influences its genetics and evolution (Nehm 2018), a code shared by almost a fourth of respondents. For instance, their response places "a living organism" as the subject of evolution, implying that each individual can drive its own evolution, with deliberate decisions that can impact what genetic changes they pass on to their offspring, and thus has the ability to choose whether to evolve or not or choose how to evolve. Other students also demonstrated this non-normative view of evolution. For example, one wrote that evolution is "the ability of an organism to make genetic changes over long periods of time in order to adapt and survive in changing environments," while another wrote that "adaptations [are] made by the living creature in order to survive." Both these quotes suggest that individual organisms have an ability to change their individual genotype or phenotype and thus drive their own evolution through a conscious, deliberate choice. Indeed, we highlight the significant overlap in student responses that included both the "agency/intentionality" and "change within an individual" codes, indicating that many students are likely holding this naïve view of evolution as being driven by conscious, deliberate choices in an individual that then leads to genetic changes in their offspring.

These responses, where students view individuals as having the agency to change and evolve or as the main drivers of their own evolution, appear to align with teleological and Lamarckian ideas of evolution, which are both non-normative conceptions of evolution that are still nevertheless found commonly in novice learners when thinking about selection (Cunningham and Wescott 2009; Gregory 2009; Gregory and Ellis 2009; Hartelt et al. 2022; Steinwachs and Martens 2022). Teleological thinking – where students often ascribe a 'need' for evolution and anthropomorphize organisms – can lead to students characterizing natural selection as a need-based evolutionary force, though such thinking may be context dependent and instructors can re-frame such student thinking into more normative ways of thinking about evolution though using metacognitive prompts or other strategies that make students aware of the human biases often leading to teleological thinking (González Galli et al. 2020; Gouvea and Simon 2018; Varella 2018). Similarly, Lamarckian ideas of evolution have also been characterized as 'need-based' evolution, centering around the inheritance of acquired traits based upon the use/disuse of traits (Bishop and Anderson 1990; Cunningham and Wescott 2009; Stover and Mabry 2007). While many of our responses were ambiguous in nature and may not have fully aligned with teleological or Lamarckian ideas, the frequency of the 'agency/intentionality' and 'change within an individual' codes suggest that many students likely hold these non-normative ideas about evolution at the beginning of introductory biology.

Other students characterized evolution as change without specifying what they viewed as changing. "Evolution is the changing of life and environment over time," one student wrote, providing an unclear response of what they meant by "life" changing, while several others wrote that evolution is "change over time." These responses are broad and do not illuminate if these students think that individual organisms are changing, or if they are thinking about evolutionary change at the population or species level. It is possible, too, that students do not have clear, concrete conceptions of what is changing when thinking about evolution. Similarly, such responses do not provide any insight into *how* students think change occurs, aligning with past work that has found that novice learners often struggle to provide mechanistic, causal explanations of evolutionary change (Abrams and Southerland 2001). In addition, very few students (less than 6%) were able to conceptually connect evolutionary processes at different scales (e.g., connecting how changes in an individual, such as a mutation occurring, could lead to evolution in the population), again highlighting that students may not have deep conceptual knowledge of how evolutionary processes occur, or that such conceptual knowledge did not come to mind when asked to define what evolution is. Taken together, these responses suggest that many students associate evolution with change but may have gaps in their knowledge construction of what processes lead to this evolutionary change.

Students rarely connect evolution to genetics or genetic change

Indeed, understanding evolutionary processes requires an understanding that evolution, at its core, involves genetic change, i.e., changes in allele frequency in a population (Herron and Freeman 2007). However, very few students (less than 15%) brought up DNA, genes, alleles, or genetic variation in their responses, with even fewer responses that indicate students connected evolutionary change across multiple levels (i.e., explicitly connecting between genetics and changes in physical traits, etc.). These results suggest that many students entering introductory biology have not constructed mental models of evolution that incorporate genetic changes. Indeed, past work has identified that nearly all of the most commonly used undergraduate biology textbooks segregate evolutionary concepts from other biological principles and do not integrate evolutionary concepts within the sections that introduce genetics, suggesting that students may be compartmentalizing their mental models of evolution and DNA and may not be forming connections between these concepts (Nehm et al. 2009). Our results reinforce this idea that many students may have gaps in their mental models of evolution and may not be able to fully integrate the role of DNA and genetics in evolutionary processes.

In addition, many students who are prompted to think about genetics and evolution still hold misconceptions about genetics and students often struggle to comprehend the genetic nature of variation, even after instruction (Andrews et al. 2012; Bray Speth et al. 2014). Non-normative ideas about genetics were seen in our responses, even for students who attempted to connect evolution and genetics. For example, one student wrote that "evolution happens over a very long period of time (hundreds of years to hundreds of thousands of years) to a specific species of organism. It basically occurs when traits are passed down from one organism to the next. After a long time, the genes that are the most beneficial to a species become the most dominant among all of the members in that species." This response indicates that the student is connecting the concept of evolution with genetic change in a population, but incorrectly ascribes the main cause for genetic changes as due to differences in fitness while not recognizing the role of other evolutionary mechanisms (e.g., mutation, gene flow, and genetic drift) in causing genetic changes in a population. Similarly, the student misuses the word "gene" (instead of the more accurate term of "allele") and the word "dominant" when referring to the allele with highest frequency in a population. This use of the word "dominant" may stem from the student using the word in its vernacular meaning, but may also indicate that the student is thinking that alleles that are dominant in nature (i.e., those alleles that override recessive alleles) are more frequent in a population, a documented misconception among students learning evolution (Abraham et al. 2014; Nehm and Reilly 2007). Similarly, other students used imprecise language when referring to genetic concepts, likely leading to additional barriers for forming deep conceptual connections between evolution and genetics. For instance, one student wrote that evolution is "changes in frequency of DNA at a population level," using the general term of "DNA" instead of the more precise definition that evolution is the change in frequency of alleles, or specific variants of DNA. The student's response is not correct given that evolution does not involve changes in the amount of DNA (i.e., evolution does not relate to the concentration of DNA in an individual), but rather the frequency of specific allelic variants within a population, an important nuance when thinking about evolution. Our results here align with past work that has identified that many students are not able to conceptually link DNA and evolution (Jaksetic 2012) and that students can often have trouble conceptualizing or differentiating key genetics terms such as "gene" or "allele", particularly given the many different contexts for such terms in undergraduate biology courses (Gericke and Hagberg 2010; Mills Shaw et al. 2008; Pashley 1994).

Students often view evolution and natural selection synonymously or hold a strong connection between evolution and natural selection

In addition to lacking connections between evolution and genetics, most students also highlighted natural selection or adaptation in their definitions of evolution. These responses – combined with the paucity of responses that referred to mutations (less than 4%), random genetic drift (0%), migration/gene flow (0%), or recombination (0%) – suggest that many students view evolution and natural selection as synonymous, or that many students see a strong association between evolution and natural selection, but not between evolution and the other evolutionary forces. Indeed, many students attempted to provide only a definition of selection, indicating that they may view evolution and selection as equivalent conceptually, with virtually no students conveying that natural selection is only one of multiple forces that lead to evolution. Indeed, the emphasis on students thinking about evolution through the lens of natural selection often persists beyond introductory biology. For instance, upper-division evolution students still often hold the misconception that selection is the dominant force of evolution, often neglecting to think about other evolutionary forces (Price and Perez 2016), and many upper-division students often translate misconceptions about natural selection to the other evolutionary forces as well (Andrews et al. 2012; Price et al. 2014; Price and Perez 2016). Other work has similarly found that students rarely cite non-adaptive evolutionary mechanisms even after instruction on random genetic drift (Beggrow and Nehm 2012).

In addition, nearly a fourth of students characterized evolution through the lens of survival of organisms. The majority of these responses either explicitly or implicitly described differential survival of organisms due to the presence of adaptations in some members of a population, a normative response that conceptually links evolution, selection, and the differential survival of organisms. "Evolution is the progression of species through natural selection," one student wrote, directly equating evolution and natural selection and not recognizing that evolution encompasses change through multiple evolutionary mechanisms. "If a feature a creature has gives them an advantage to survive, even if very slight, over the course of a long period of time this advantage will help them reproduce and pass down those genes and eventually the feature that helped them survive becomes standard among their species." This response contains scientifically accurate ideas about natural selection, with the student correctly describing how adaptations that increase fitness will likely increase in frequency in a population. However, not all responses that described evolution through the lens of survival highlighted differential survival within a population. "Evolution is the gradual change in a species across a large timespan which should facilitate successful survival of member organisms," one student wrote. This student – in contrast to the first student who recognized that selection centers around differential survival (and reproduction) of individuals in a population – viewed evolution in the context of species survival. Their response does not mention selection explicitly, nor does it mention a mechanism of evolution, other than conveying that they believe (incorrectly) that evolution must contribute to survival of an organism.

Many students view evolution as leading to progress or describe perceived consequences of evolution

While most students defined evolution as a process, many students also highlighted what they perceived as the results, or consequences, of evolution. For example, nearly a fourth of students indicated that they believed evolution would lead to 'progress' of species, including an increase in complexity or an advancement of the species. "Evolution is the idea or concept of an entity or species progressing forward, adapting, and or evolving into something better and or more practical for whichever situation they may encounter," one student wrote, while another commented that evolution "is the progress of a species' intelligence as they continue to interact with a variety of environments." These statements align with past work that has found that students often hold misconceptions that evolution can only benefit species or that evolution must lead to more complex, advanced organisms (Gregory and Ellis 2009; Tidon and Lewontin 2004; Werth 2012). There were, however, some responses that incorporated more normative ideas about evolution even though the student associated evolution with progress. "Evolution is the progression of species through natural selection," one student wrote. "If a feature a creature has gives them an advantage to survive, even if very slight, over the course of a long period of time this advantage will help them reproduce and pass down those genes and eventually the feature that helped them survive becomes standard among their species." This response, while conveying a naïve concept of natural selection leading to a "progression of [the] species", correctly identifies that natural selection is driven by differential survival and reproduction and changes in the gene pool over time.

Interestingly, while some of these responses included students' perceived explanations for *why* organisms evolve and progress (i.e., an explanation of evolutionary process), many of these responses did not highlight a mechanism of change and instead only described the perceived result of evolution. While it is possible that some of these students may hold normative mechanisms of evolutionary change, the lack of causal explanations in these responses suggests that some of the students may have incomplete mental models of evolution. For instance, the response that evolution is "the progress of a species' intelligence" only focuses on the consequences of evolution, and hints that this consequence is a result of "interact[ing] with a variety of environments." However, the student does not provide any causal reasoning for *why* or *how* organisms may evolve when interacting with the environment, instead focusing solely on the perceived results of evolution.

Other students define evolution through the lens of speciation

Similarly, other students characterized evolution through the lens of speciation, focusing on the formation of new species as a product or consequence of evolution. "Evolution is the natural engine of organic research and development on Earth," one student wrote. "It is a collection of processes and events that give rise to new species over time." Similarly, another student stated that "evolution is the process of development of new 'upgraded' species throughout preexisting species," not only defining evolution as speciation but also indicating a non-normative conception of evolution leading to progress. These responses illustrate how these students define evolution as the formation of new species but do not provide any conceptual framework for what may cause this speciation and do not provide any details on what they think the processes are that lead to speciation. Instead, these students focus on the cognitive entity of the perceived result of evolution, i.e., the formation of new species. Others, however, provided a more normative, mechanistic explanation for speciation. "Evolution is an extensive and slow process that occurs over thousands of years. This process is driven by natural selection and the environment which leads to the alteration and divergence of species," one student wrote. Though there are other mechanisms besides selection that can lead to speciation, the student provides a correct mental model that suggests that divergent selection can lead to speciation. While there have been multiple past misconceptions documented about speciation (Balgopal 2014; Catley and Novick 2009; Heddy and Sinatra 2013), these results are the first we are aware of that indicates that some students may be equating evolution with speciation, or may most strongly associate speciation with evolution when prompted "what is evolution?".

Student conceptions on speed of evolution

Almost a fifth of students viewed evolution as a slow, gradual process that takes significant time to occur. "Evolution is a slow and gradual change in an organism in response to some stimulus," one student wrote. This student conveys an incorrect, non-normative conception of evolution as always being slow and gradual in their response. Similarly, other students conveyed their understanding that evolution can only occur over the span of many years. "Evolution is when something undergoes an adaptation to a difficulty that the organism has encountered that takes millions of years," one student wrote, while another commented that "evolution occurs over the course of many years and its where there is a constant change happening within species." These responses indicate that undergraduate students entering introductory biology often commonly think of evolution as a slow, gradual process, aligning with past work that has found this misconception across undergraduate students (Andrews et al. 2012; Nelson 2008). In addition, past work has found that students often struggle thinking about the different time scales of evolution, often having trouble conceptualizing evolution as a process that can occur both rapidly and gradually, depending on the study system and scale of evolution (Orraryd and Tibell 2021). Our results suggest that the students entering introductory biology in our study may also have trouble thinking about evolution as a process that can be either gradual or sudden, depending on context, scale, and evolutionary processes at play, and that many students likely enter introductory biology only thinking about evolution as a gradual, slow process.

Few students use the phrases 'descent with modification' or 'survival of the fittest' when describing evolution

Intriguingly, we note that very few students (less than 2%) included the phrase 'descent with modification' in their response, despite this phrase being used by Charles Darwin to describe evolution (Penny 2011). Similarly, less than 4% used the phrase 'survival of the fittest', a phrase first coined by Herbert Spencer to expand upon Darwin's ideas of natural selection (Offer 2014), though a substantial number of students described evolution through the lens of survival and/or natural selection. While these two phrases have entered common academic parlance in the discourse about evolution and the history of evolutionary thought, it appears that these phrases either have not substantially influenced students' conceptions of evolution or that students are not repeating these phrases when asked to characterize evolution, suggesting that students may not be directly associating evolution with these phrases.

Students view evolution similarly across institutions, but instruction may shape students' definitions of evolution

Interestingly, we found only minimal differences among student conceptions of evolution between students at the two institutions, suggesting that students entering introductory biology at the two- and four-year institutions are likely viewing evolution similarly and that students' alternate conceptions of evolution are likely prevalent regardless of institution type. We also found minimal differences between student conceptions of evolution between the first- and second-semester introductory biology courses at both institutions. However, we found that students entering second semester introductory biology at the four-year institution had a larger percentage of students highlighting genetic variation and defining evolution through the lens of survival compared to students entering the first-semester introductory biology course, suggesting that specific instruction in the first-semester introductory biology course may have shaped students' conceptions of evolution. While the first-semester introductory course at this institution focuses primarily on cellular and molecular biology, the course includes a lab where students learn about natural selection through simulating survival of individuals with different traits and learn about the requirements for selection (including the need for variable traits to be heritable). Given that many students in the second-semester introductory biology course have previously taken the first-semester introductory biology course, we speculate that this instruction may have led to the increase in the number of students viewing evolution through the lens of survival. There was also a non-significant increase in the number of students who viewed evolution through the lens of natural selection (from 45.0 to 67.3%), suggesting that additional students were equating evolution with natural selection caused by differential survival of individuals after taking the first-semester introductory biology course.

Students in non-STEM general biology view evolution similarly to students in majors' introductory biology

Our study also demonstrated that students starting the non-STEM majors' general biology at the two-year college largely viewed evolution in similar ways as students in the STEM majors' introductory biology course. While we were only able to compare between non-majors and majors introductory biology at the two-year college given that the four-year university we sampled does not offer a general biology course geared toward non-STEM majors, our results highlight that both STEM and non-STEM majors may enter college with similarly naïve conceptions of evolution. The only difference was that the students in the non-STEM course were more likely to associate evolution with natural selection than students in the STEM course. We speculate that this difference may be due to STEM majors being potentially previously exposed to other evolutionary mechanisms (e.g., mutation) in high school biology courses, while non-STEM majors may not have had these same experiences.

Future directions for biology education research community

Our work leads to several potential future research questions for the biology education research community. For instance, it remains unclear what factors shape these student conceptions of evolution, and why some students focus more on evolutionary processes while others instead emphasize perceived consequences of evolution. Similarly, future work is needed to investigate how students construct their mental models of evolution after receiving instruction in introductory biology and other biology courses, and if there are differences in students' understanding and acceptance of evolution based on their initial characterization of evolution upon entering introductory biology. Past work has revealed that students may hold many interconnected conceptions about evolution, so changing a student conception in one area may require conceptual changes in other areas (Demastes et al. 1996). As a result, more work is needed to examine the connections between the different conceptions of evolution we uncovered. Finally, our work reveals that students often are not conceptually linking evolution with genetic changes, and there is an urgent need for more work that develops and assesses integrated curricular approaches in both secondary and post-secondary education that can promote deeper student conceptual understanding of evolution and genetics.

Implications for instructors

Our work has several implications for biology instructors at both the secondary and post-secondary levels:

- **Be explicit in defining evolution and emphasize other evolutionary processes beyond just natural selection.** Our work reveals that students are commonly associating evolution with only natural selection, with students often using these terms interchangeably, and that students are not recognizing the breadth of other evolutionary forces such as random genetic drift, migration, mutation, or recombination. Even the few students who acknowledge other evolutionary mechanisms may incorrectly believe that selection is the primary force driving evolution, not recognizing the importance of the other evolutionary forces. We highlight how the BioCore Guide, a resource that presents a list of important biological statements aligned with the *Vision & Change* core concepts, includes all of the evolutionary mechanisms and not just selection (Brownell et al. 2014). We thus echo other calls for biology instructors to emphasize the presence of other evolutionary mechanisms beyond selection, and to integrate the discussion of multiple evolutionary mechanisms when first introducing and discussing evolution, including in introductory biology courses (Price and Perez 2016). Instructors may consider incorporating examples of evolutionary change through other mechanisms beyond selection to illustrate how evolution can occur even without selection.

- **Address evolutionary misconceptions through active learning and targeted instruction.** Our work found that students are coming into undergraduate introductory biology courses with a range of incorrect conceptions about evolution, including equating evolution with natural selection, viewing evolution in a teleological and Lamarckian manner, and characterizing evolution as a slow and gradual process. Past work has identified that instruction that uses active learning that is specifically designed to promote correct conceptual thinking leads to higher rates of learning about evolution (Nehm et al. 2022). Similarly, past work has also shown that reasoning about evolution is strongly influenced by context, such as the examples used to describe evolutionary phenomena (Gouvea et al. 2023). Thus, instructors can design active-learning based activities that build students' conceptual models of evolution through the use of targeted examples from various contexts that draw upon students' existing conceptions (Gouvea 2023; Gouvea et al. 2023). For instance, the authors of this paper begin our evolution courses by asking students to define evolution, then providing a scientific definition of evolution drawn from the textbook used for the course. For example, the Herron and Freeman *Evolutionary Analysis* textbook defines evolution as "changes in allele frequency over time" (Herron and Freeman 2007). Students are then asked to compare their definitions with the scientific definitions and then apply these definitions to various scenarios that illustrate different evolutionary forces at work. Through this activity, students are guided to recognize any potential misconceptions in their past characterizations of evolution and can reflect upon evolutionary change in a variety of contexts. Instructors may wish to refer to published papers that compile helpful resources and strategies for addressing students' evolutionary misconceptions (e.g., Alters and Nelson 2002; Nelson 2008). Similarly, instructors can leverage existing naïve student conceptions of evolution to guide students to construct more accurate models of evolution, an approach suggested by multiple education research papers (Duit and Treagust 2003; Hammer 2000; Maskiewicz and Lineback 2013). For example, we identified that many students incorrectly associated evolution with a gradual process. When discussing evolutionary mechanisms, such as selection and drift, instructors could explicitly ask students to consider what factors would impact how "fast" evolutionary processes act, and then discuss concepts such as strength of selection (which would influence how quickly a given trait changes in frequency due to selection) and population size (which would impact influence of drift). This type of approach can change the situational context behind a student's reasoning and promote a deeper understanding of evolutionary processes (Gouvea et al. 2023).
- **Integrate genetics and evolution instruction throughout secondary and post-secondary biology courses, and explicitly connect micro- and macroevolution.** Our results show that the majority of students are not thinking of DNA or genetics when defining or characterizing evolution, suggesting disconnects between their mental models of genetics and evolution. These results align with past work that has found that most textbooks segregate evolutionary principles from other biological concepts, despite evolution being a unifying theme throughout biology (Nehm et al. 2009). This segregation of topics potentially contributes to students struggling to form cohesive mental models of evolution and may inadvertently make connecting microevolutionary processes (i.e., changes in allele frequency) with macroevolutionary changes more challenging to understand (Nehm et al. 2009; Wilensky and Novak 2010). Thus, we encourage instructors to integrate genetics and evolution instruction and explicitly connect microevolution and macroevolution so that students can more easily see the connections between these biological ideas. Instructors may wish to consult a helpful paper that provides suggestions and curricular examples that integrate concepts from genetics and evolution (Kalinowski et al. 2010) as well as curricular resources (e.g., computer simulations) that are designed to connect microevolution and macroevolution (Wilensky and Novak 2010).
- **Clarify the use of the term 'evolution'.** Finally, we see that students may be conceptualizing the term

'evolution' in different ways or providing different associations with evolution when prompted, with some students most directly associating the term with evolutionary processes while others are primarily referring to the consequences of evolution. Instructors may wish to directly acknowledge these potential differing conceptions of evolution and discuss how this term can encompass a wide variety of biological concepts. We note that many introductory biology courses often cover disparate evolutionary ideas, such as evolutionary processes, the origin of life, biodiversity, and both micro- and macroevolution, all under the label of 'evolution', and spending time clarifying the breadth of evolution and what this term means may facilitate students' construction of their mental models of evolution.

Limitations and conclusion

We acknowledge several limitations of our work. First, our work is limited to two institutions near each other, and further work will be needed to determine if students at other institutions, particularly those with different institutional profiles than the ones we sampled, hold the same range of conceptions. In addition, our work was based upon analyzing fortuitous data collected from an in-class activity which was not designed as a study, meaning that our data is limited to one time point and that we are not able to compare how students from different demographics view evolution. We also highlight how there were different response rates among the two institutions, which we speculate is due to a larger number of instructors teaching the introductory biology courses at the two-year institution, leading to potentially greater variation in the amount of time provided for each class to complete the activity. This variance may have contributed to the lower response rates than at the four-year institution. Similarly, our data was limited to one question asked in an in-class activity, and we were limited to the responses that students provided, which may not have reflected a student's breadth of knowledge about evolution but may instead reflect what terms or concepts they most directly associated with evolution during the first day of class. We did not include any follow-up interviews or deploy concept inventories to further explore student conceptions of evolution, meaning that we are limited in evaluating the extent of students' knowledge of evolution, evolutionary processes, genetics, or other related. In addition, we acknowledge that the situation context and specific item features of a problem may have a large impact on how students respond to a given question about evolution (de Lima and Long 2023; Federer et al. 2015; Heredia et al. 2016; Nehm and Ha 2011; Nehm and Ridgway 2011; Schmiemann et al. 2017), and thus it is possible that questions similar to the one used in our in-class activities but with different framings may have generated differing responses. For instance, we relied on our in-class activity asking "what is evolution?" as a way for instructors to capture student thinking about evolution and reveal how students may be defining evolution, but it is possible that other phrasings of the question (e.g., "how would you define evolution?", or "how would a biologist define evolution?") may have caused students to write different responses.

Despite these limitations, our work provides the first investigation of how students characterize and define evolution prior to instruction in an introductory biology class that we are aware of and provides a valuable examination of student thinking that complements past work that has focused more on student thinking of specific evolutionary concepts (e.g., natural selection). Our work thus contributes to the existing evolution education literature by directly examining how students characterize evolution, providing insights into how students may develop alternate conceptions about different evolutionary principles. In addition, our work provides one of the first comparisons of student thinking about evolution we are aware of that includes students at a two-year college and a non-research intensive four-year university as well as students enrolled in both STEM and non-STEM introductory biology courses. Given that most biology education research has been conducted in the context of large, research-intensive universities (Lo et al. 2019), our work provides a unique perspective by examining perspectives from over 300 students at a private, comprehensive four-year university as well as a two-year college.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12052-024-00208-x.

Supplementary Material 1

Acknowledgements

We thank the instructors at Irvine Valley College and Chapman University who used this activity, as well as the students for participating.

Author contributions

All three authors analyzed the data; JLH wrote the first draft of the manuscript, and all authors were involved in editing and revising the paper.

Funding

This work is unfunded.

Data availability

Anonymized data are available upon request.

Declarations

Ethical approval

All activities were approved by both the Chapman and Irvine Valley College Institutional Review Boards.

Competing interests
The authors declare no competing interests.

Received: 10 April 2024 / Accepted: 7 August 2024
Published online: 23 August 2024

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