Chapter 34
Student Learning Across Course Instruction in Genetics and Evolution

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Abstract Genetics and evolution are interconnected topics — evolutionary change requires inheritance and correspondingly, genetic variation is required for selection to have any impact on a population. However, misconceptions and naive ideas of both genetic and evolutionary concepts can fundamentally impact a student's understanding of biology. It is therefore important to understand what information students obtain in various courses at the undergraduate level, and how knowledge of concepts in one course might impact learning in another course. This is particularly important with respect to genetics concepts, as Genetics courses are often a prerequisite to Evolution courses and serve frequently as students' introduction to the basic concepts that underlie evolution. This study compared student performance related to key genetics concepts after taking both Fundamental Genetics and Evolution courses to taking Fundamental Genetics alone and tracked student performance as they progressed through the Genetics-Evolution course sequence. We created a 16-question assessment, developed from published literature on these topics, and administered the survey at three timepoints: the end of Fundamental Genetics, the beginning of Evolution and again at the end of the Evolution course. Our data suggest students do complete Fundamental Genetics with a few misconceptions related to genetic information pertinent to evolution, and that these concepts are varyingly

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corrected by taking Evolution. This research highlights the advantages of both tracking and comparing students as they progress through a Genetics-to-Evolution course sequence, particularly with respect to how faculty can leverage course sequencing to improve student performance.

34.1 Introduction

In *On the Origin of Species* (1859) [19], Darwin devotes an entire chapter to the Laws of Variation and further explores the importance of variation, and the link between traits in parents and offspring in *The Variation of Animals and Plants Under Domestication* (1868) [20]. Despite a clear role for inheritance in natural selection, Darwin was unable to provide an adequate model [14]. It was not until the discovery of the work of Gregor Mendel that a particulate inheritance hypothesis was accepted [35]. Mendel, however, understood the importance of his work to evolution [35], writing "This seems to be the one final way of finally reaching a solution to a question whose significance for the evolutionary history of organic forms cannot be underestimated [35]."

Although Darwin was able to articulate his theory of natural selection using a faulty model (pangenesis and blended inheritance), it was clear by the 1920's that the application of Mendel's work (Mendelian inheritance) supported evolution by natural selection [14]. In particular, the idea that mutations in genes provide new sources of variation on which selection acts forms the basis for evolutionary change.

The link between evolution and genetics is clearly emphasized in our current approaches to teaching and learning in biology. *Vision and Change in Undergraduate Biology*, the core structural advisement from the American Association for the Advancement of Science (AAAS), lists evolution as a core concept in biology [31]. Specifically, *Vision and Change* recognizes the evolution and diversity of life on Earth as not only critical to understanding biology, but also inherently a function of genetic processes. Although the core foundational idea of evolution originally developed prior to the genetics and genomics era, we know that [genetic] inheritance is an important component to student understanding of evolution [39]. Despite the clear intertwined nature of evolution and inheritance, most biology majors take separate courses in genetics and evolution, and student understanding of these two topics is not evaluated together.

Prior research suggests a positive relationship between evolution acceptance and genetics understanding [36], but the role of genetics instruction in understanding evolutionary processes is unclear despite studies exploring student understanding of genetics [4, 15, 32, 53]. Moreover, student understanding of genetics can include a litany of incorrect ideas, from issues of relationships between genes, chromosomes and cells, to the transmission and display of traits [4, 15, 32]. Particularly resistant incorrect ideas may not change after instruction [53], thus persisting as a student makes their way through the curriculum.

An understanding of evolution, likewise, eludes many students at all levels: K-12 [22, 37]; lower-level undergraduate (both biology majors and non-majors [6, 39, 52]; and upper-level undergraduate [9, 17, 18, 27, 58]. Naïve mental models can plague student understanding as they advance to higher-level courses [5], and as with concepts in genetics, misconceptions can often persist even after instruction [10, 41]. If left uncorrected, these misconceptions continue to manifest themselves as undergraduates progress through the (often linear-pathed) biology curricula.

Recent work has argued that teaching genetics before evolution may increase student understanding of evolution, because the concepts of mutations and alleles can be translated into allele frequency change [34]. Using a common garden experiment, where the order of modules on genetics and evolution were swapped, Mead [34] found that lower-performing students scored better in both genetics and evolution understanding when genetics was taught first. However, the study investigated the order of genetics and evolution in a single class of secondary students. Most post-secondary institutions introduce evolution and genetics in introductory courses that include coverage of the concept that heritable genetic variation is critical for population evolution. However, the need for mastery of these processes for a complete understanding of evolution may not be emphasized and at most institutions, upper-level courses in genetics and evolution are emphasized, and taught separately. Rarely do undergraduates take courses in population or quantitative genetics.

Furthermore, at many institutions, students are expected to take an upper level Genetics course prior to taking an upper level Evolution. In an informal survey conducted via the Evoldir community listserv, of 123 institutions worldwide, 6% list courses in Genetics and Evolution as co-required, 49% list Genetics as a prerequisite to Evolution, 41% have no defined relationship between the courses, and 4% have other. Furthermore, despite its central role in biology, most of the 4% indicated Evolution was not offered as a stand-alone course. Thus, even with evidence suggesting genetics knowledge may improve evolution understanding, roughly only half the institutions in our sample mandate Genetics prior to Evolution, and nearly an equal number make no clear recommendation for the order of these courses and most likely do not emphasize the connection between the two.

Students learn by integrating new knowledge into existing knowledge frameworks [47, 2]. If existing and new knowledge are incompatible, naive ideas can interfere with students' ability to understand new information as they progress through courses, particularly if frameworks are not reorganized or replaced [21, 48, 51]. Curricular frameworks must therefore be carefully crafted such that the requisite knowledge is not only presented, but sufficiently mastered over several experiences, and concepts covered in one course linked to those in follow-up courses [13, 16, 43, 55].

The National Research Council (NRC) advocates for basing curricula on empirical evidence for how students reason and develop competence in the domain [1]. Yet research is lacking to show how genetics knowledge prepares students to conceptualize evolution, specifically whether students can adequately link the underlying genetic characters of a population to its evolution. As Nehm and Ridgway have shown [40], even "emerging expert" students seem to accurately describe natural

selection but lack the incorporation of non-adaptive mechanisms, such as genetic drift, present in true expert models of evolution [3, 24, 30, 45, 46].

Because naive ideas can originate prior to explicit instruction, and these ideas tend to persist throughout learning, it is important to understand what information (and misinformation) students obtain as they progress through course sequences. Particularly with respect to Evolution and Genetics, learning should be tracked to determine what information students learn in Genetics, and what is added or replaced by taking Evolution, particularly as Genetics is a mandatory prerequisite at many institutions and introduces many fundamental evolutionary genetics ideas. With the goal of tracking and elucidating student learning of genetic concepts important to understanding evolution, our research explored three questions: 1) Which genetic concepts important for understanding evolution do students understand following Genetics and Evolution coursework, compared to taking a Genetics course alone? 2) For students who take these courses immediately one after the other, does their understanding of the concepts change between the end of Genetics and the beginning of Evolution, and after a full course on Evolution? 3) Do students maintain any specific misconceptions after instruction in either course, and if so, which topics appear to be the most difficult for students?

34.2 Methods

34.2.1 Courses of Focus

This study concerned student performance at a large Midwestern university in relation to enrollment in two courses: Genetics (Fall 2012) and Evolution (Spring 2013). Genetics is a large (300 students) traditional lecture course with 3 exam-based assessments and a cumulative final. Evolution is a considerably smaller course (50-75 students), and is also an upper level course, with both a lecture and a recitation. Both Genetics and Evolution courses require completion of a cell and molecular biology course, and Evolution requires completion of Genetics. Concepts covered in both courses align with expectations outlined by the biology education community [54]. Assessments in Evolution are a combination of exams, quizzes, homework, in-class discussion, and a final exam. The syllabi for each course suggest course coverage includes the genetic basis of evolution, population genetics, and gene expression in explanations of genetic variation. And while not required as a prerequisite for either Genetics or Evolution, many students do complete one semester of an introductory biology course that covers biological diversity and organismal biology, including principles of evolution, transmission genetics, population biology, community structure and ecology.

34.2.2 Study Population

Prior to completing the study's assessments in both Fundamental Genetics and Evolution, students were asked to give consent to participate in this study (x12-1182e). We administered surveys to students enrolled in Fundamental Genetics during the Fall 2012 semester. We then administered the same assessment to students enrolled in Evolution; we will refer to these participants as 'comparison students'. To track a cohort of students as they complete the course sequence (hereafter 'tracked students'), student data were matched across Fundamental Genetics and Evolution; these students took Evolution immediately following Fundamental Genetics ($N = 18$). Students who failed to complete assessments in their entirety were not included in these analyses. Table 34.1 provides demographics for the study population. GPA and ACT scores were self-reported.

Table 34.1: Demographic information of participants for each of the groups compared. The number of female and non-white, non-Hispanic students are shown as percentages. Year in College, GPA, and ACT score are shown as averages.

Criteria	Student Completing Genetics Only	Student Completing Genetics and Evolution	Tracked Students
Female	48.10%	75%	83.3%
Non-white, Non-Hispanic	30.0%	5.0%	0%
Year in College	3.96	3.78	3.61
GPA	3.66	3.74	3.83
ACT Score	26.38	27.89	27.75

34.2.3 Survey Design

Our assessments consisted of a number of survey questions assessing class demographics and prior course performance, followed by a series of sixteen questions assessing student knowledge of course-related topics. Questions were taken directly from the genetics assessment literature, specifically the Genetics Literacy and Assessment Instrument (GLAI) [11], Genetic Drift Inventory (GeDI) [49], and the Genetics Assessment For Core Understanding (GCA) [54], and course textbooks (Pearson's Mastering Biology Sequence; Campbell et al. 2008; see Table 34.2 [12]). Questions were either multiple choice with each distractor tied to a specific misconception, or agree/disagree format coupled with fill-in-the-blank formats to explain why a particular answer was given. Questions were chosen to test basic understanding of the fundamental genetic underpinnings of evolution, span several Bloom levels [7], and correspond to documented misconceptions.

Table 34.2: Question Sources and Concepts Measured in this Assessment.

General Concept/Learning Goal	Item number on current assessment	Original test item
Interpret results from molecular analyses to determine the inheritance patterns and identifies of human genetics that can mutate to cause disease	1	GCA No.19
Extract information about genes, alleles, and gene functions by analyzing the progeny from genetic crosses	2	GCA No.4
Compare different types of mutations and describe how each can affect genes and the corresponding mRNAs and proteins	3	GCA No.5
Most human traits, including diseases, result from the products of multiple genes interacting with environmental variables; examples include height, heart disease, cancer, and bipolar disorder	4	GLAI No.3
Understanding Mendelian patterns of inheritance, and their biological basis, allows probability statements about the occurrence of traits in offspring	5	GLAI No.7
Occasional errors in DNA structure and replication result in genetic variation	6	GLAI No.15
Occasional errors in DNA structure and replication result in genetic variation	7	GLAI No.9
Understanding Mendelian patterns of inheritance, and their biological basis, allows the probability of trait occurrence in offspring to be predictive of parental traits	8	Mastering Biology
Occasional errors in DNA structure and replication result in genetic variation	9	Mastering Biology
Understanding Mendelian patterns of inheritance, and their biological basis, allows probability statements about the occurrence of traits in offspring	10	Mastering Biology
Genetic drift can be a driver of evolution, not just natural selection	11	GEDI
The magnitude of the effect of random sampling error for genetic drift from one generation to the next depends on the population size	12	GEDI
Random sampling error tends to cause a loss of genetic variation within populations, which in turn increases the level of genetic differentiation among populations	13	GEDI
Mutation and genetic drift can contribute to genetic variation in a population	14	GEDI
Standing genetic variation in a population can be acted on by selection	15	GEDI
Genetic drift can create genetic differences between populations over time	16	GEDI

34.2.4 Survey Assessment Administration

The assessment was administered at three curricular timepoints: at the end of Fundamental Genetics (to establish a baseline), at the beginning of Evolution (to determine knowledge retained following Fundamental Genetics and prior to Evolution), and at the end of Evolution (to examine learning and retention of nave ideas). All students consenting to the study completed the assessments within the initial (in the case of Evolution pre-test) and final week of the semester (in the case of the post-Genetics and post-Evolution tests). Assessments at each time point were identical, and students were not given feedback about the accuracy of their responses at any time.

Regardless of the accuracy of their responses, students were incentivized with extra credit for the completion of the assessment at the end of Genetics (N=224; 70.22% participation rate). Because of a reduced class size as students transition into a much smaller Evolution course and the need to keep sample sizes high (N =38; 69.09% participation rate), only students who completed both the pre-and post-tests within Evolution were compensated, although two chose to complete the post-assessment without having completed the pre-assessment.

34.2.5 Survey Assessment Analysis

Prior to scoring, all assessment responses were de-identified, and in the case of the tracked students, matched with prior assessment responses. Individual item performance was compared for both students in the comparison and tracked populations. In addition to scoring answers as correct/incorrect, we further examined student responses for questions that were consistently incorrect. Finally, items that showed improvement across administration of the assessments were noted as possibly the result of additional instruction in evolution.

34.3 Results

34.3.1 Statistical Analyses

Several statistical models were chosen based on the questions asked and statistical agreement with model assumptions; however a significance cut off of $p = 0.05$ was used for all statistical tests. All tests were run in R (R Core Team, 2013, version 3.0.2 [50]).

To assess our instrument, we first conducted a series of Item Response Theory (IRT) tests, and the performance results that follow are reflecting the use of the assessment survey instrument. We partition our performance analyses into two parts:

Part 1 addresses 'comparison' students (comparing those who complete both Genetics and Evolution to those who complete only Genetics); and Part 2 addresses 'tracked' students (following a cohort to document how student knowledge changes as students progress through the course sequence).

Table 34.3: Item performance (expressed as percent of students answering a question correctly) for students who took only Genetics and students who took both Genetics and Evolution. Total average score and standard error for samples are also included.

Question	Students who took only Genetics	Students who took both Genetics and Evolution
1	89.0%	91.7%
2	38.8%	47.2%
3	54.0%	91.7%
4	90.8%	94.4%
5	89.3%	100%
6	68.4%	52.8%
7	73.3%	86.1%
8	87.4%	88.9%
9	54.9%	86.1%
10	58.7%	50.0%
11	54.9%	69.4%
12	65.0%	80.5%
13	75.0%	91.7%
14	87.0%	88.9%
15	86.0%	88.9%
16	85.0%	97.2%
Average Score	*12.77*	*13.05*
SE	*0.20*	*0.41*

34.3.2 Instrument Analysis

Rasch analyses were conducted on the overall instrument to examine both the difficulty of the items and conceptual independence of the items. Item Characteristic Curve (ICC) plots revealed independence of the items. From a graphical model check plotting the predictive ability of each question, question 5 appeared to deviate from the parameter estimates of the remaining questions. Therefore, an Andersons' likelihood ratio test for goodness of fit with mean-split criterion was performed to determine if this question violated invariance of the model estimates for the instrument; the results supported inclusion of all questions in the instrument for analysis

(*Andersen LR-test, LR-value= 22.642, df= 14, p = 0.066*). Figure 34.1 provides a summary of item difficulty and parameter distribution.

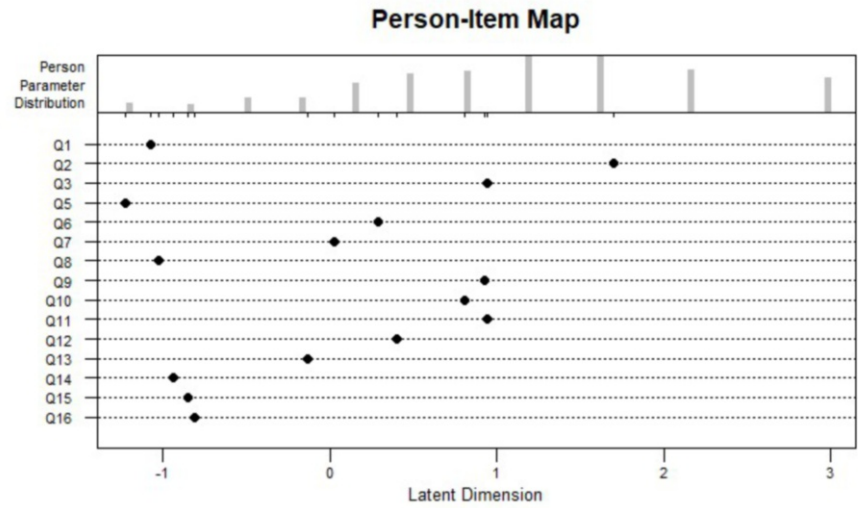

Fig. 34.1: Item difficulties for each of the 16 questions in the assessment. The upper panel displays student performance on the instrument, and the lower panel shows the difficulty of each item. Constructed based on the total number of respondents in the study and, in the case of repeated testing, used only on the first assessment taken by the individual ($N = 262$).

34.3.3 Part 1: Comparing Students between Courses

To compare students taking only Genetics to those taking both Genetics and Evolution, a multiple logistic regression model was conducted with course (either post-Genetics or post-Evolution), gender, year in college, GPA, ACT scores, and race predicting the sum of correct responses. Two-way interaction terms were added to the original model one at a time to examine which combination of predictors yielded the best model based on AIC values. Main effects and interactions, even when not significant, were retained through model selection for the lowest (best) AIC model. When accounting for gender, year in college, GPA, ACT score, and race, students who complete both Genetics and Evolution score higher on our overall assessment than students who have only completed Genetics ($\beta = 0.55310, SE = 0.22135, p = 0.01315$; see Table 34.4). Thus, taking both Genetics and Evolution results in higher scores on genetics concepts compared to taking Genetics alone.

We also examined four questions that appeared to be missed most often. Responses suggested students either had a lack of knowledge, held a misconception, or

Table 34.4: Multivariate regression model predicting the sum of the correct responses.

	β	SE	t	p	$exp(\beta)$
Survey	0.55310	0.22135	2.499	0.01315*	1.738634
Gender	0.15587	0.30993	0.503	0.61550	1.168674
Year in college	-0.12183	0.22119	-0.551	0.58230	0.8852989
GPA	0.215	0.220	0.975	0.331	1.239862
ACT score	0.22203	0.21801	1.018	0.30953	1.248609
Race	-0.94765	0.35912	-2.639	-0.00888**	0.3876509

performed better following the Evolution course. We identified two "lack of knowledge" questions: one concerning translating genotype to phenotype using a Punnett Square (Question 10, Supplemental Material) and one concerning genetic drift as a non-adaptive mechanism of evolution (Question 11, Supplemental Material). Students struggled to translate genotype to phenotype using a Punnett Square. Correct responses were not predicted by Gender, Year, GPA, ACT score, nor race as main effects ($p > 0.11$ in all cases), however, adding the interaction term of Year*ACT to this model shows year in college, ACT score, and the interaction of ACT and year as significant predictors of a correct response (Table 34.5). Similarly, students struggled to identify genetic drift as a non-adaptive mechanism of evolution (Question 11, Supplemental Material). However, increased ACT scores are a significant predictor of a correct response ($\beta = 0.08346, SE = 0.04025, p = 0.0381$), although no other significant variables or interactions were found (all $p > 0.05$).

Table 34.5: Logistic regression model predicting the response to question 10 with interaction terms.

	β	SE	z	p	$exp(\beta)$
Survey	-0.26170	0.20083	-1.303	0.192537	0.7697419
Gender	0.44579	0.28002	1.592	0.111388	1.561723
Year in college	4.72143	1.54968	3.047	0.002314**	112.3288
GPA	0.13764	0.19626	0.701	0.483092	1.147562
ACT score	0.57159	0.17366	3.291	0.000997***	1.771081
Race	-0.44350	0.32182	-1.378	0.168165	0.6417862
Year*ACT	-0.16937	0.05548	-3.053	0.002265**	0.8441965

One question displayed a clear misconception: defining a mutation (Question 2; Supplemental Material). Gender ($\beta = 0.90309, SE = 0.28538, p = 0.001553$) and year in college ($\beta = 0.43755, SE = 0.20584, p = 0.033527$) were significant predictors of a correct response. Substantively, this means that the odds of a correct response were 2.47 times higher for men than for women, and 1.55 times higher for those further along in school than those less far along in school. All two-way

interactions were again explored between the predictors, but none turned out to be significant (all $p > 0.05$).

Students who take Evolution after Genetics improved specifically in their knowledge of standing genetic variation (Question 9; Supplemental Material). Students who completed both Evolution and Genetics were 2.38 times more likely to provide correct answers to this question compared to students who only completed Genetics ($\beta = 0.86593, SE = 3.086, p = 0.00203$). Subsequent analysis revealed that two interactions were significant in the best model by AIC: year*ACT and GPA*ACT. When both interaction terms are included in the model, neither emerges as a significant predictor of a correct response (perhaps because both involve the ACT variable and thus introduce high levels of multi-colinearity into the model).

34.3.4 Part 2: Tracking Students across Courses

We were able to track a total of 18 students from the end of Genetics through to the end of Evolution. Table 34.6 provides a summary of the performance on each item for each of the three time points. In addition, to examine student performance as they progressed through the course sequence, repeated measures ANOVA, ANCOVA and Generalized Estimating Equations (GEE) were used. First, we conducted a repeated measures ANOVA using the Greenhouse-Geisser correction for violations of sphericity. In this model, survey (whether post-Genetics, pre-Evolution, and post-Evolution) was our within-subjects factor to test whether a statistically significant change was observed in the sum survey score over time. Note that an ANCOVA was performed to examine whether ACT score influenced survey outcomes in interactions and is reported where appropriate. Figure 34.2 depicts the overall mean change in the sum of correct responses across surveys, which was not found to be significant (Repeated measures ANOVA with Greenhouse-Geisser correction, $F(1.612, 25.788) = .776, p = .445$).

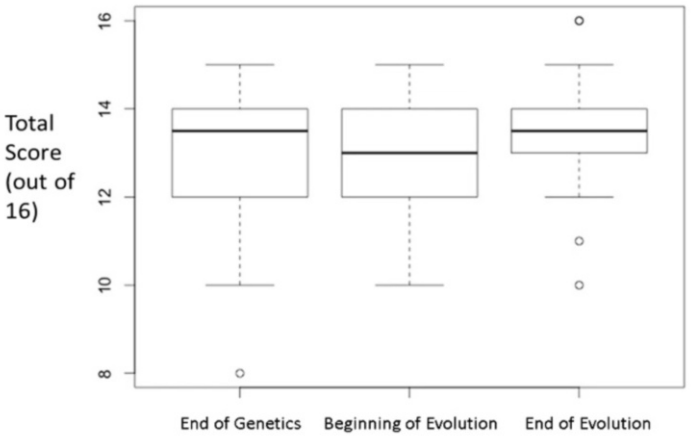

Fig. 34.2: Boxplot of the Sum of Correct Responses Across Time. Central boxes represent values from the lower to upper quartile (25 to 75 percentile; first and third quartiles), and are intended to give an approximate 95% confidence interval for differences in the two datasets. Bold lines represent the median, and extreme values are represented by open circles.

Finally, the remaining models examined how the odds of getting a correct answer on a given survey question changed over time. Because repeated measures AN(C)OVA cannot be used for binary dependent variables (such as whether a question is right or wrong) which violate its assumptions (linearity, constant variance, and normality, etc.) and logistic regression cannot be used due to the non-independence that exists within subjects, we chose a generalized estimating equations (GEE) model. This model met the model assumptions and converged better than the alternative multilevel model with random effects for subject and time (which account for within-subjects dependencies). The correlation structure for each GEE model was set to be "unstructured", meaning that the correlations between time points were estimated from the data. This is the most relaxed assumption one can make about the within-subjects correlations and ideal to use in the absence of specific predictions for changes between consecutive surveys.

The two questions identified above as connected to a lack of knowledge for comparison students were also found to be a challenge for the tracked students. Namely, students struggled in translating genotype to phenotype and in identifying genetic drift as a non-adaptive mechanism of evolution. However, among our tracked students, data suggested students taking the sequence contiguously may be better at defining the term "mutation" (Question 2; Supplemental Material). Of the four incorrect responses, 76% initially stated that mutations must alter the amino acids; these responses slowly convert to the correct response over time, that a mutation is any change in the genetic code. However, this improvement was not ultimately strong enough to be significant ($B = .329, SE = .244, p = .18, OR = 1.39$).

Table 34.6: Overall per item performance on the assessment (as expressed by percent correct per question), as well as the score average and SD of overall assessment for students at 3 curricular timepoints.

Question	End of Genetics	Beginning of Evolution	End of Evolution
1	83.0%	77.8%	94.4%
2	33.0%	44.4%	50.0%
3	67.0%	83.3%	94.4%
4	88.9%	94.4%	100%
5	100%	94.4%	100%
6	77.8%	66.6%	55.6%
7	83.3%	77.7%	88.9%
8	100%	72.2%	88.9%
9	66.7%	83.3%	88.9%
10	55.6%	44.4%	44.4%
11	61.1%	61.1%	66.7%
12	94.0%	83.3%	83.3%
13	94.0%	66.7%	94.4%
14	94.0%	88.9%	100%
15	88.9%	88.9%	94.4%
16	100%	94.4%	100%
Average Score	*12.89*	*12.94*	*13.44*
SE	*0.47*	*0.33*	*0.35*

However, a significant improvement was seen among the tracked students with respect to their understanding of the importance/role of standing genetic variation ($B = .689, SE = .347, p = .047, OR = 1.99$; Question 9; Supplemental Material). Among this group, a GEE model also indicated a significant interaction between survey and ACT scores ($B = .095, SE = .046, p = .041$), where scores tend to increase more across the surveys with increasing ACT score.

34.4 Discussion

Students performed adequately on the overall assessment, averaging about 75-80% correct responses across the assessment. Our results suggest that in general, taking a course in Genetics followed by a course in Evolution can help students retain genetic concepts important to understanding evolution. However, our tracking of a subset of students through this course sequence suggests the specific advantages can be hard to identify.

It is important to note that tracked student scores did not appear to change appreciably from the end of Genetics to the beginning of Evolution; although this is the

most ideal case of back-to-back courses, we can confirm students are not immediately 'forgetting' concepts from semester to semester, and it is possible that student ideas on these topics may be formed prior to taking their Genetics course, and their Genetics and Evolution courses may only serve to cement certain ideas, rather than correct and replace them.

Introductory Biology experiences, for example, may cover this material [8, 10, 28, 39, 57, 59]. Students in introductory biology courses do tend to harbor the same naive ideas about evolution, focusing on the organismal and less on the molecular basis of evolution and rarely connecting how phenotypic diversity arises from genetic variation caused by mutation [56, 57]. As experts consistently include heredity and genetic variation in explanations of evolutionary change [40], it appears gains on these topics can occur, but they are modest and likely a result of specific instructional methods [57]. If these specific interventions which lead to gains are missing from one's educational background, regardless of if in introductory biology or the courses since, naive ideas may persist (see [26, 39]).

Indeed, students explanations of evolutionary phenomena frequently do not include genetic concepts like variation and heredity, even after explicit instruction [40, 41, 42, 57]. The inferences necessary to 'see' mutation as a mechanism may be particularly challenging [16, 25], in addition to the inherent difficulties of understanding natural random processes [23, 29, 33]. For this reason, some concepts may be inherently more difficult and deserve more attention in the curriculum.

We observed similar difficulties in our students specifically, defining mutations, recognizing the importance of standing genetic variation, translating genotypes to phenotypes, and identifying genetic drift as a non-adaptive force of evolution. Following an Evolution course, however, students did appear to improve in recognizing the importance of standing genetic variation in populations. The concepts of defining mutations, translating genotypes to phenotypes, and recognizing genetic drift as a force of evolution continued to be problematic even following a course in Evolution. As these courses are often the last of the upper-level required courses for majors, many students may therefore be graduating with an incomplete understanding of the genetics underlying evolution.

Somewhat heartening, however, is the fact that some improvement can happen. Among our tracked students, the data suggest that students may grow better at defining a mutation. Originally, students assumed most commonly that mutations must change amino acids to qualify as a mutation, but gradually students widened their definition to include general genetic changes, such as those to noncoding regions. Grasping that mutations need not have phenotypic effects underscores how modern phylogenies are often constructed and evolutionary relationships are determined. Repeated exposures to the concept of a mutation and phylogeny by integrating evolution into courses may help students to link genetic variation to organismal variation.

It is also possible that there are 'ceiling effects' in the scores attainable on the assessment, as the scores among the tracked students appeared to be consistent, with just the variation narrowing at the end of Evolution as lower-scoring students improved. Repeated exposure could be the mechanism by which under-performing stu-

dents improve, offering students multiple chances to demonstrate mastery. However, because these questions were generally multiple choice and coded as correct or not, we may be missing progressively more accurate models of evolutionary thinking as the students advance in the curriculum [40, 41], particularly for lower-performers, who may be prone to having multiple areas of improvement. Explicit tests, potentially at more refined intervals with more open-ended responses [10, 38, 39, 44] or oral interviews [41] should be used to address what misconceptions exist and compare gains made across the curriculum in detail.

Longitudinal research on where and how misconceptions arise and change throughout the curriculum (from Introductory Biology on) will guide the development of curricula and make evident where department-level changes need to be made. Our method of tracking students through the curriculum provides a starting point from which instructors can begin to compare and track student performance as they progress through the curriculum as designed, and make modifications if necessary. Because tracking can be difficult to do in practicality, particularly as it can take more time and student schedules and class sizes are variable, we advocate the combination of approaches of tracking students as well as direct comparisons between students in these courses. A better understanding of the gains made, and for whom and when, will help the field in developing how learning progressions intersect in genetics and evolution curricula.

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References

1. How people learn: Brain, mind, experience, and school: Expanded edition. National Research Council by National Academies Press (2000)
2. Knowing what students know: The science and design of educational assessment. National Research Council by National Academies Press (2001)
3. Ackermann, R.R., Cheverud, J.M.: *Detecting genetic drift versus selection in human evolution*. Proceedings of the National Academy of Sciences **101**(52), 17,946–17,951 (2004)
4. Agorram, B., Clement, P., Selmaoui, S., Khzami, S.E., Chafik, J., Chiadli, A.: *University students' conceptions about the concept of gene: Interest of historical approach*. US-China Education Review, ISSN 1548-6613, USA **7**(2), 9–15 (2010)
5. Alters, B.J., Nelson, C.E.: *Perspective: Teaching evolution in higher education*. Evolution **56**(10), 1891–1901 (2002)
6. Anderson, D.L., Fisher, K.M., Norman, G.J.: *Development and evaluation of the conceptual inventory of natural selection*. Journal of Research in Science Teaching **39**(10), 952–978 (2002)
7. Anderson, L.W., Krathwohl, D.R., Airasian, P.W., Cruikshank, K.A., Mayer, R.E., Pintrich, P.R., Raths, J., Wittrock, M.C.: *A taxonomy for learning, teaching, and assessing: A revision*

of Bloom's taxonomy of educational objectives, abridged edition. White Plains, NY: Longman (2001)
8. Andrews, T., Price, R., Mead, L., McElhinny, T., Thanukos, A., Perez, K., Herreid, C., Terry, D., Lemons, P.: *Biology undergraduates' misconceptions about genetic drift*. CBE - Life Sciences Education **11**(3), 248–259 (2012)
9. Balgopal, M.M., Montplaisir, L.M.: *Meaning making: What reflective essays reveal about biology students' conceptions about natural selection*. Instructional Science **39**(2), 137–169 (2011)
10. Bishop, B.A., Anderson, C.W.: *Student conceptions of natural selection and its role in evolution*. Journal of Research in Science Teaching **27**(5), 415–427 (1990)
11. Bowling, B.V., Acra, E.E., Wang, L., Myers, M.F., Dean, G.E., Markle, G.C., Moskalik, C.L., Huether, C.A.: *Development and evaluation of a genetics literacy assessment instrument for undergraduates*. Genetics **178**(1), 15–22 (2008)
12. Campbell, N.A., Reece, J.B., Urry, L., Cain, M., Wasserman, S., Minorsky, P., Jackson, R.: *Biology*. Pearson Benjamin Cummings, New York (2008)
13. Carey, S.: *The origin of concepts*. Oxford University Press, New York (2009)
14. Charlesworth, B., Charlesworth, D.: *Darwin and genetics*. Genetics **183**(3), 757–766 (2009)
15. Chattopadhyay, A.: *Understanding of genetic information in higher secondary students in northeast india and the implications for genetics education*. Cell Biology Education **4**(1), 97–104 (2005)
16. Chi, M.T., Slotta, J.D., De Leeuw, N.: *From things to processes: A theory of conceptual change for learning science concepts*. Learning and Instruction **4**(1), 27–43 (1994)
17. Dagher, Z.R., BouJaoude, S.: *Scientific views and religious beliefs of college students: The case of biological evolution*. Journal of Research in Science Teaching **34**(5), 429–445 (1997)
18. Dagher, Z.R., Boujaoude, S.: *Students' perceptions of the nature of evolutionary theory*. Science Education **89**(3), 378–391 (2005)
19. Darwin, C.: *On the origin of species by means of natural selection*. John Murray (1859)
20. Darwin, C.: *The variation of animals and plants under domestication*, vol. 2. John Murray (1868)
21. Demastes, S.S., Settlage Jr, J., Good, R.: *Students' conceptions of natural selection and its role in evolution: Cases of replication and comparison*. Journal of Research in Science Teaching **32**(5), 535–550 (1995)
22. Donnelly, L.A., Kazempour, M., Amirshokoohi, A.: *High school students' perceptions of evolution instruction: Acceptance and evolution learning experiences*. Research in Science Education **39**(5), 643–660 (2009)
23. Garvin-Doxas, K., Klymkowsky, M.W.: *Understanding randomness and its impact on student learning: Lessons learned from building the Biology Concept Inventory (BCI)*. CBE - Life Sciences Education **7**(2), 227–233 (2008)
24. Gould, S.J., Lewontin, R.C.: *The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme*. Proc. R. Soc. Lond. B **205**(1161), 581–598 (1979)
25. Hmelo-Silver, C.E., Marathe, S., Liu, L.: *Fish swim, rocks sit, and lungs breathe: Expert-novice understanding of complex systems*. The Journal of the Learning Sciences **16**(3), 307–331 (2007)
26. Hokayem, H., BouJaoude, S.: *College students' perceptions of the theory of evolution*. Journal of Research in Science Teaching **45**(4), 395–419 (2008)
27. Ingram, E.L., Nelson, C.E.: *Relationship between achievement and students' acceptance of evolution or creation in an upper-level evolution course*. Journal of Research in Science Teaching **43**(1), 7–24 (2006)
28. Kalinowski, S.T., Leonard, M.J., Andrews, T.M.: *Nothing in evolution makes sense except in the light of DNA*. CBE - Life Sciences Education **9**(2), 87–97 (2010)
29. Klymkowsky, M.W., Garvin-Doxas, K.: *Recognizing student misconceptions through Ed's Tools and the Biology Concept Inventory*. PLoS Biology **6**(1), e3 (2008)
30. Lande, R.: *Natural selection and random genetic drift in phenotypic evolution*. Evolution **30**(2), 314–334 (1976)

31. Ledbetter, M.L.S.: *Vision and change in undergraduate biology education: A call to action presentation to Faculty for Undergraduate Neuroscience, July 2011*. Journal of Undergraduate Neuroscience Education **11**(1), A22 (2012)
32. Lewis, J., Wood-Robinson, C.: *Genes, chromosomes, cell division and inheritance - Do students see any relationship?* International Journal of Science Education **22**(2), 177–195 (2000)
33. Mead, L.S., Scott, E.C.: *Problem concepts in evolution part II: Cause and chance*. Evolution: Education and Outreach **3**(2), 261–264 (2010)
34. Mead, R., Hejmadi, M., Hurst, L.D.: *Teaching genetics prior to teaching evolution improves evolution understanding but not acceptance*. PLoS Biology **15**(5), e2002,255 (2017)
35. Mendel, G.J.: *Versuche über Pflanzen-Hybriden? [Experiments Concerning Plant Hybrids]? [1866]*. Verhandlungen des naturforschenden Vereines in Brünn (1865)
36. Miller, J.D., Scott, E.C., Okamoto, S., et al.: *Public acceptance of evolution*. Science **313**(5788), 765 (2006)
37. Moore, R., Brooks, D.C., Cotner, S.: *The relation of high school biology courses & students' religious beliefs to college students' knowledge of evolution*. The American Biology Teacher **73**(4), 222–226 (2011)
38. Nehm, R.H., Beggrow, E.P., Opfer, J.E., Ha, M.: *Reasoning about natural selection: Diagnosing contextual competency using the ACORNS instrument*. The American Biology Teacher **74**(2), 92–98 (2012)
39. Nehm, R.H., Reilly, L.: *Biology majors' knowledge and misconceptions of natural selection*. AIBS Bulletin **57**(3), 263–272 (2007)
40. Nehm, R.H., Ridgway, J.: *What do experts and novices "see" in evolutionary problems?* Evolution: Education and Outreach **4**(4), 666–679 (2011)
41. Nehm, R.H., Schonfeld, I.S.: *Measuring knowledge of natural selection: A comparison of the cins, an open-response instrument, and an oral interview*. Journal of Research in Science Teaching **45**(10), 1131–1160 (2008)
42. Nieswandt, M., Bellomo, K.: *Written extended-response questions as classroom assessment tools for meaningful understanding of evolutionary theory*. Journal of Research in Science Teaching **46**(3), 333–356 (2009)
43. Ohlsson, S.: *Resubsumption: A possible mechanism for conceptual change and belief revision*. Educational Psychologist **44**(1), 20–40 (2009)
44. Opfer, J.E., Nehm, R.H., Ha, M.: *Cognitive foundations for science assessment design: Knowing what students know about evolution*. Journal of Research in Science Teaching **49**(6), 744–777 (2012)
45. Orr, H.A.: *Testing natural selection vs. genetic drift in phenotypic evolution using quantitative trait locus data*. Genetics **149**(4), 2099–2104 (1998)
46. Parker, G.A., Smith, J.M.: *Optimality theory in evolutionary biology*. Nature **348**(6296), 27 (1990)
47. Piaget, J.: *Success and understanding*. Harvard University Press, Cambridge, MA. (1978)
48. Posner, G.J., Strike, K.A., Hewson, P.W., Gertzog, W.A.: *Accommodation of a scientific conception: Toward a theory of conceptual change*. Science Education **66**(2), 211–227 (1982)
49. Price, R.M., Andrews, T.C., McElhinny, T.L., Mead, L.S., Abraham, J.K., Thanukos, A., Perez, K.E.: *The genetic drift inventory: A tool for measuring what advanced undergraduates have mastered about genetic drift*. CBE - Life Sciences Education **13**(1), 65–75 (2014)
50. R-Core-Team: *R: A language and environment for statistical computing* (2013)
51. Sinatra, G.M., Brem, S.K., Evans, E.M.: *Changing minds? Implications of conceptual change for teaching and learning about biological evolution*. Evolution: Education and Outreach **1**(2), 189–195 (2008)
52. Sinatra, G.M., Southerland, S.A., McConaughy, F., Demastes, J.W.: *Intentions and beliefs in students' understanding and acceptance of biological evolution*. Journal of Research in Science Teaching **40**(5), 510–528 (2003)
53. Smith, M., Knight, J.: *Using the genetics concept assessment to document persistent conceptual difficulties in undergraduate genetics courses*. Genetics **191**, 21–32 (2012)

54. Smith, M.K., Wood, W.B., Knight, J.K.: *The genetics concept assessment: A new concept inventory for gauging student understanding of genetics*. CBE - Life Sciences Education **7**(4), 422–430 (2008)
55. Smith III, J.P., DiSessa, A.A., Roschelle, J.: *Misconceptions reconceived: A constructivist analysis of knowledge in transition*. The Journal of the Learning Sciences **3**(2), 115–163 (1994)
56. Speth, E.B., Long, T.M., Pennock, R.T., Ebert-May, D.: *Using Avida-ED for teaching and learning about evolution in undergraduate introductory biology courses*. Evolution: Education and Outreach **2**(3), 415–428 (2009)
57. Speth, E.B., Shaw, N., Momsen, J., Reinagel, A., Le, P., Taqieddin, R., Long, T.: *Introductory biology students' conceptual models and explanations of the origin of variation*. CBE - Life Sciences Education **13**(3), 529–539 (2014)
58. Tran, M.V., Weigel, E.G., Richmond, G.: *Analyzing upper level undergraduate knowledge of evolutionary processes: Can class discussions help?* Journal of College Science Teaching **43**(5), 87–97 (2014)
59. White, P.J., Heidemann, M., Loh, M., Smith, J.J.: *Integrative cases for teaching evolution*. Evolution: Education and Outreach **6**(1), 17 (2013)

Supplemental Material

Instrument

1. Polydactyly is an inherited trait that results in extra fingers or toes. In the United States 0.1% of the population exhibits polydactyly. People with polydactyly have the genotype Pp, where P represents the allele that causes polydactyly and p represents the normal allele of this gene. Which of the following is true?

a) The P allele is more frequent in the US than the p allele.
b) The P allele is less frequent in the US than the p allele.
c) The two alleles, P and p are at approximately equal frequencies in the US population.
d) There is not enough information to answer this question.

2. Suppose that a single DNA base change of an A to a T occurs and is copied during replication. Is this change necessarily a mutation?

a) Yes, as it is a change in the DNA sequence of an organism.
b) Yes, but it must be a base change occuring in gametes.
c) Yes, but it must be a base change occuring in the coding part of a gene.
d) Yes, but it must be a base change that alters the amino acid sequence of a protein.
e) Yes, but it must be a base change that alters the appearance of the organism.

3. An isolated population of prairie dogs has longer than average teeth. As a result they can eat more grass with less effort and are better able to survive and reproduce. The mutation(s) that resulted in longer teeth:

a) allowed the teeth to grow longer over several generations until they reached an optimal length for eating grass.
b) arose in many members of the population simultaneously and then lead to longer teeth.
c) happened as a result of chance within the prairie dog population and then lead to longer teeth.
d) occurred because the prairie dogs needed to be more efficient at eating grass to survive and reproduce.
e) would only occur in a prairie dog population that eats grass and would not occur in a population that lives on seeds.

4. Adult height in humans is partially determined by our genes. When environmental conditions are held constant, humans have a wide variety of heights (not just short, medium, and tall). Height is probably influenced by:

a) one gene with two alleles.
b) a single recessive gene.
c) a single dominant gene.
d) several genes and alleles.
e) only paternal genes.

5. Sometimes a trait seems to disappear in a family and then reappear in later generations. If neither parent has the trait, but some of the offspring do, what would you conclude about the inheritance of the trait?

a) Both parents are carriers of the recessive form of the gene.
b) Only one parent has two copies of the recessive form of the gene.
c) Only one of the parents has a dominant form of the gene.
d) Only one parent has a copy of the recessive form of the gene.
e) It is most likely the result of new mutations in each parent.

6. Which of the following is a characteristic of mutations in DNA?

a) They are usually expressed and result in positive changes for the individual.
b) They are usually expressed and cause significant problems for the individual.
c) They occur in the body cells of a parent and are usually passed onto offspring.
d) They usually occur at very high rates in most genes of all known organisms.

e) They usually result in different versions of a gene within the population.

7. Mutations in DNA occur in the genomes of most organisms, including humans. What is the most important result of these mutations?

a) They produce new genes for the individual.
b) They produce new enzymes for the individual.
c) They provide a source of new cells for the individual.
d) They provide a source of variation for future generations.
e) They produce new chromosomes for future generations.

8. In peas, the round allele is dominant over the wrinkled allele. If a plant with round peas is crossed to a plant with wrinkled peas, all of the resulting plants have round peas. What is the genotype of the parents in this cross?

a) $Rr \times Rr$
b) $RR \times rr$
c) $rr \times rr$
d) $Rr \times rr$
e) $RR \times Rr$

9. Which of the following is a true statement concerning genetic variation?

a) It tends to be reduced by the processes involved when diploid organisms reproduce.
b) It arises in response to changes in the environment in which the organism lives.
c) It is creased by the direct action of natural selection on the population.
d) It must be present in the population before natural selection can act upon it.
e) High average heterozygosity populations predict less genetic variation.

10. Black fur in mice (B) is dominant to brown fur (b). Short tails (T) are dominant to long tails (t). What fraction of the progeny of crosses $BbTt \times BBtt$ will be expected to have black fur and long tails?

a) 3/16
b) 8/16
c) 6/16
d) 9/16
e) 1/16

Please read the following statements to answer questions 11-16.

A small island is home to a unique population of land snails. This population was founded by 10 individuals that floated to the island on a log, and it has been isolated from the large mainland population ever since.

A. Biologists compared the genetic variation of the mainland and island populations a few years after colonization. Please indicate whether a biologist would agree or disagree with each of the following statements.

11. The biologists observed genetic drift but not evolution because the island snails were just as well-suited to their environment as the ones on the mainland.

A. Agree ***B. Disagree***

Why?

12. The biologists observed genetic drift and concluded that the island population had fewer versions of each gene than the mainland population.

A. Agree ***B. Disagree***

Why?

B. After forty generations, biologists measured the genetic variation of the island snail population again. They concluded that the population of snails on the island had remained isolated and that genetic drift had occurred. Please indicate whether a biologist would agree or disagree with each of the following statements about the processes that contributed, at least in part, to genetic drift in the population of island snails.
Please indicate whether a biologist would agree or disagree with each of the following statements about what occurred during the forty generations since colonization.
13. The island population experienced random changes in the frequency of certain traits that made them genetically distinct from the mainland population.

A. Agree ***B. Disagree***

Why?

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14. The island population may have experienced mutation in addition to random changes in the frequency of certain traits.

A. Agree ***B. Disagree***

Why?

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15. The island population may have adapted to conditions on the island if random genetic change increased survival and reproduction of some individuals.

A. Agree ***B. Disagree***

Why?

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16. The island and mainland populations will be less similar to each other than they were 100 generations ago.

A. Agree ***B. Disagree***

Why?

With what gender do you most identify?
Male
Female
Prefer not to Answer

What year are you in school?

What is your overall GPA?

What semester did you/are you taking Genetics?

What was your approximate SAT or ACT score? (score corrected for ACT)

With what race/ethnicity do you most identify?

American Indian/Alaskan Native
Asian
Black/African American
Native Hawaiin/Other Pacific Islander
White (Not Hispanic or Latino)
White (Hispanic or Latino)
Other (text entry)