

Crossing the Threshold: Bringing Biological Variation to the Foreground

Janet M. Batzli,^{†*} Jennifer K. Knight,[‡] Laurel M. Hartley,[§] April Cordero Maskiewicz,^{||} and Elizabeth A. Desy[¶]

[†]Biology Core Curriculum (Biocore), University of Wisconsin–Madison, Madison, WI 53706;

[‡]Department of Molecular, Cellular, and Developmental Biology, University of Colorado, Boulder,

CO 80309; [§]Department of Integrative Biology, University of Colorado Denver, Denver, CO 80217;

^{||}Department of Biology, Point Loma Nazarene University, San Diego, CA 92106; [¶]Department of Science, Southwest Minnesota State University, Marshall, MN 56258

ABSTRACT

Threshold concepts have been referred to as “jewels in the curriculum”: concepts that are key to competency in a discipline but not taught explicitly. In biology, researchers have proposed the idea of threshold concepts that include such topics as variation, randomness, uncertainty, and scale. In this essay, we explore how the notion of threshold concepts can be used alongside other frameworks meant to guide instructional and curricular decisions, and we examine the proposed threshold concept of *variation* and how it might influence students’ understanding of core concepts in biology focused on genetics and evolution. Using dimensions of scientific inquiry, we outline a schema that may allow students to experience and apply the idea of variation in such a way that it transforms their future understanding and learning of genetics and evolution. We encourage others to consider the idea of threshold concepts alongside the *Vision and Change* core concepts to provide a lens for targeted instruction and as an integrative bridge between concepts and competencies.

INTRODUCTION

What concepts are centrally important to students’ understanding of biology but difficult to teach and learn in the context of introductory biology? Specifically, are there concepts so integral to the discipline that, without mastery, students cannot move forward to gain a deeper understanding of a topic? These questions galvanized our group of biology educators to explore the recent literature on *threshold concepts* and transformational learning. In this essay, we 1) provide a brief introduction to candidate threshold concepts specific to biology, 2) use *variation* as a possible exemplar threshold concept to demonstrate how one might bring this tacit concept to the foreground in a curriculum, and 3) pose implications for instruction and research questions regarding threshold concepts in biology that deserve dialogue within the biology education community.

As biology educators with expertise in genetics, ecology, and evolutionary biology, our group initially came together to discuss crosscutting concepts that were integrative and bridged our subdisciplines. We subsequently discovered a literature base focused on “threshold concepts” and the proposal that there exist domain specific concepts that, when mastered, can transform learning. This idea of “threshold concepts” originated with the foundational papers of Meyer and Land (2003) and Meyer *et al.* (2006). While much of the support for the existence of threshold concepts is currently based on interviews of subject experts and students, we find the idea of such concepts provocative and potentially fruitful. As such, we put forth this essay to spark discussion within the biology education research community. If threshold concepts do exist, then they deserve attention in the context of reimagining biology curricula. For example, threshold concepts could provide targets for instruction and offer integrative learning opportunities in alignment with the core concepts outlined in *Vision and Change in Undergraduate*

Jennifer Momen, *Monitoring Editor*

Submitted October 15, 2015; Revised June 15, 2016; Accepted June 21, 2016

CBE Life Sci Educ December 1, 2016 15:es9

DOI:10.1187/cbe.15-10-0221

*Address correspondence to: Janet M. Batzli (jcbatzli@wisc.edu).

© 2016 J. M. Batzli *et al.* CBE—Life Sciences Education © 2016 The American Society for Cell Biology. This article is distributed by The American Society for Cell Biology under license from the author(s). It is available to the public under an Attribution–Noncommercial–Share Alike 3.0 Unported Creative Commons License (<http://creativecommons.org/licenses/by-nc-sa/3.0>).

“ASCB®” and “The American Society for Cell Biology®” are registered trademarks of The American Society for Cell Biology.

Biology Education: A Call to Action (American Association for the Advancement of Science [AAAS], 2011). We offer this essay not as an exhaustive review of threshold concepts literature, nor as evidence for the existence of threshold concepts, but rather as a summary of our thoughts for how proposed threshold concepts might connect with our collective work in biology education research and curriculum development.

DEFINING THRESHOLD CONCEPTS

Meyer and Land (2003; also see Meyer *et al.*, 2006) coined the term “threshold concepts,” defining it as a set of concepts held by experts that are central to reasoning, integration, and mastery in a discipline. Meyer and Land argue that threshold concepts are portal ideas that open up a “previously inaccessible way of thinking about, understanding, interpreting, or viewing something without which the learner cannot progress” (Meyer *et al.*, p. 3). Despite limited empirical evidence for “threshold crossing,” there is a growing literature base,¹ primarily from the United Kingdom and Australia, that has begun to identify and gather evidence for threshold concepts in an array of disciplines. Threshold concepts are characterized by the following qualities: they are *transformative*—causing a shift in a learners’ perception of a subject; *irreversible*—once they are understood, the learner is unlikely to forget them; *integrative*—connecting multiple domains; *bounded*—applicable within a discipline and having specific meaning to experts in that discipline; *frequently troublesome*—challenging, counterintuitive, and problematic due to confusion of ideas, misconceptions, or naïve conceptions; and *discursive*—associated with use of specific disciplinary language through discourse (Meyer and Land, 2003; Meyer *et al.*, 2006; Davies and Mangan, 2007; Kinchin, 2010; Baillie *et al.*, 2013). In addition to these qualities, the development of understanding may be associated with a *liminal state* wherein the learner can waver between previously held incorrect ideas and more accurate thinking about a concept. Through this oscillation, a learner may experience dissonance, confusion, and a state of transitional knowledge followed by clarity that often accompanies entry into a community of practice (e.g., from learner of biology to biologist; Cousin, 2009). The idea of threshold concepts is concordant with conceptual change theory whereby movement through and beyond a threshold is a transformational process for the learner (Posner *et al.*, 1982; Davies and Mangan, 2007). For the purpose of our essay, we consider the idea of threshold concepts as a helpful heuristic through which instructors could effectively evaluate and revise curricula.

Threshold concepts in biology have been described by several authors, namely Taylor (2006, 2008), who, through a series of faculty interviews, proposed the following topics that meet some or all of the characteristics of a threshold concept: energy transformation, probability and uncertainty, variability, scale, and hypothesis generation. Taylor further divides threshold concepts into process concepts (e.g., energy transformation) and abstract concepts (e.g., uncertainty, scale, variability). Ross *et al.* (2010) integrates Taylor’s list of threshold concepts (e.g., variation, probability, uncertainty, scale, randomness) with those within standard content (e.g., genetics, evolution,

ecology, cellular metabolism) to propose a model in which threshold concepts can be applied, revisited, and threaded as a web throughout the curriculum to promote transformational learning. These foundational papers helped guide the identification of threshold concepts in interdisciplinary biosciences such as biochemistry (Loertcher *et al.*, 2014).

Although most of the threshold concepts proposed in Ross *et al.* (2010) resonated with our group, we were uncertain about the empirical basis for identifying them. Ideally, if a researcher concludes that particular concepts are indeed “threshold concepts,” the claim should be grounded in empirical evidence or at least be supported by existing studies of student learning. Barradell (2013) and Quinlan *et al.* (2013) argue that the identification and application of threshold concepts in practice is complex and depends on the discipline and context, instructor experiences, methodologies, and mode of inquiry (i.e., positivist, constructivist, social constructivist, phenomenologist). Cousin (2009) provides a set of questions intended to help identify potential threshold concepts; however, from this and other sources (Barradell, 2013; Quinlan *et al.*, 2013), there does not yet appear to be a consistent process by which threshold concepts are identified and/or verified. Rowbottom (2007) argues that there are logical difficulties in identifying threshold concepts based on their defining characteristics, and thus it may not even be feasible to use empirical research to support or refute a claim that a concept is a threshold concept. However, we agree with Rountree and Rountree (2009), who further explain, “Even though our definitions of threshold concepts may not be perfectly precise, we can defensibly posit their existence, and agree upon their most distinctive features, until such time as we find evidence to suggest that we should retract our assertion” (p. 141).

Connections to Frameworks

One impetus for our study was to examine how threshold concepts might synergize with frameworks for learning and curriculum development. In particular, can learning progressions (National Research Council [NRC], 2007) and the core concepts and competencies outlined in *Vision and Change* (AAAS, 2011), and the “BioCore Guide” (Brownell *et al.*, 2014) be related to the proposal that threshold concepts are a gateway to mastery?

Learning progressions are described as empirically grounded and testable hypotheses about the progression of students’ understanding and use of core scientific concepts, explanations, and related practices (NRC, 2007; Corcoran *et al.*, 2009). Many learning progressions, both empirical and hypothetical, detail how learners’ understanding of a topic or concept changes over a long span of time (e.g., from fourth to 12th grade). It is not uncommon, however, for students to have difficulty moving from basic to more sophisticated levels of understanding (Mohan *et al.*, 2009; Jin *et al.*, 2013; White and Maskiewicz, 2014). In these cases, is it possible that a particularly troublesome threshold concept sits at the juncture between the two levels of understanding? Does the threshold concept, once perceived and mastered by the student, allow him or her to proceed to the next level of a learning progression? Oftentimes, moving forward in a learning progression is much more complex than understanding or applying one concept. Could it be that reaching a more sophisticated level along a learning progression

¹See online bibliography compiled and maintained by Michael Thomas Flanagan at University College London: www.ee.ucl.ac.uk/~mflanaga/thresholds.html.

requires intersection or integration of multiple threshold concepts? In support of this idea, Hartley *et al.* (2014) have previously suggested that high-level understanding of community ecology involves reasoning about variation at different scales of biological organization. If we view this research done in a learning progression context through the lens of threshold concepts, we could argue that this high-level of understanding requires an integration of two or more candidate threshold concepts such as variation and scale.

In biology, if we foreground the learning of concepts such as variation, scale, randomness, and uncertainty in curriculum, and view them through a lens of threshold concepts we could develop more effective ways to help students overcome the challenges of understanding these concepts. In particular, recognition that learning is not linear and requires liminal space for iterative exposure, application, and feedback seems essential to a curriculum emphasizing such threshold concepts. The “BioCore Guide” (Brownell *et al.*, 2014) does not mention threshold concepts specifically, but provides a framework for thinking about places in the curriculum where proposed threshold concepts might help to frame overarching principles. Triangulating threshold concepts, learning progressions, and core concepts and competencies in biology could lead to a powerful approach for curriculum development. With iterative exposure to and practice with proposed threshold concepts throughout a curriculum, we hypothesize that students could more effectively integrate core concepts and gain competency in science skills. In other words, emphasizing threshold concepts could provide targets for instruction, helping to move students along a learning progression more successfully with greater attention on integrating biology core concepts and competencies. Synergies found here could strengthen the connection between theory and practice.

Exploring Variation as a Threshold Concept

Because threshold concepts are a nascent idea with limited empirical support, and the process for identifying and verifying threshold concepts is still in development, we have chosen to focus on one proposed threshold concept in biology: variation. We describe the literature base on students’ knowledge and reasoning about variation and then propose how variation could be used to inform curriculum development and instruction in undergraduate biology courses.

Vision and Change (AAAS, 2011) suggests integrating genetics and evolution throughout the core concepts for biological literacy, stating: “Students should demonstrate an understanding that the diversity of life evolved over time by processes of mutation, selection, and genetic change.” While biologists may agree that “nothing in biology makes sense except in light of evolution” (Dobzhansky, 1973, p. 125), studies in biology education have consistently reported that students have difficulty understanding evolution (Anderson *et al.*, 2002; Nehm and Reilly, 2007; Gregory and Ellis, 2009; Smith, 2010a,b).

Perhaps one of the roots of misunderstanding about evolution lies with the proposed threshold concept of variation. Variation is key to understanding evolution but is rarely a focus of study or instruction in and of itself. In their comprehensive book about biological variation, Hallgrímsson and Hall (2005) describe how the concept of variation is essential for understanding of biology and is considered implicitly throughout the

study of biology at all scales, yet variation explicitly receives little attention as a subject of study. Ross *et al.* (2010) proposed that the underlying abstract ideas of *variation* make understanding evolution difficult. In grappling with the concept of variation, students need to integrate several interconnected processes, including recognizing that phenotypic and genotypic variation exists within populations, that variation is inherited by offspring in units (i.e., alleles), and that gene expression changes over time (development) and is modulated by both temporal and spatial environmental variation. Students’ pre-conceptions and their difficulty grasping the overarching role of variation affects not only how they make connections between key components of evolutionary processes but also how they apply their understanding to novel and complex situations in biological and ecological systems (Taylor, 2006). Nevertheless, a traditional undergraduate biology curriculum for majors often introduces evolutionary processes, assuming that students already understand variation and further assuming that students have the ability to build on this understanding in new contexts (Smith, 2010a,b).

Given that variation is key to understanding evolution, what might make it a possible threshold concept? We have observed that troublesome thinking about biological variation often comes at the novice level, when students lack observational experience and when cells and organisms are presented as essential prototypes with little recognition of the biological variation present at different scales within species. Such troublesome thinking about variation is revealed by statements such as “all mutations are bad” or “variation in science is error.” In a series of interviews with adults and children, Shtulman and Schultz (2008) asked about the variation observed *within* species and found, consistent with our anecdotal observations, that “most individuals appear to doubt that species members can, and do, vary on virtually all dimensions” (p. 1059), resulting in an inability to comprehend evolution even at the most basic level. For a deeper understanding of variation, a learner needs to become aware of the spectrum of possible values or qualities of one state in order to compare and distinguish its existence from another state (Dahlin, 2007). For example, one would need to recognize the relationships between individual organisms, populations, and species, and how they can be distinguished from one another by means of their genotypic and phenotypic variation.

As our group began to consider biological variation more closely, we found additional common misunderstandings, complexities, and relationships with other proposed threshold concepts. Price *et al.* (2013) and Garvin-Doxas and Klymkowsky (2008) found that students connect the concept of variation to randomness and uncertainty (other proposed threshold concepts) in explanations of genetic drift and natural selection. Dauer *et al.* (2013) related variation to the complex concept of scale, from the micromolecular level of allelic variation to organismal- and population-level variation. In their study, they found students gained the capacity to model and reason about variation with greater efficiency and parsimony as they gained proficiency in the language of biology and the capacity to connect complex concepts.

The concept of variation, as bounded by the discipline of biology and more specifically by the subdisciplines of genetics and evolution, is usually described using nuanced and precise

language and nomenclature (e.g., alleles, multigenic, variance, polymorphic, mutant vs. wild type, polyploidy) that is likely to be overwhelming to students. In addition, students often struggle to differentiate and articulate the levels, or scales, at which variation can act (Bahar *et al.*, 1999; Duncan and Reiser, 2007). For example, there is variation among DNA sequences, alleles, genotypes, and phenotypes, in addition to variation in gene expression during development, and variation at the organism and population level. When students gain a mastery of the language of variation and recognize that the terms are all describing variation at different dimensions and levels of biological scale, this may transform their thinking about genetics and evolution and their ability to reason about variation in a mechanistic way to explain biological phenomena.

IMPLICATIONS FOR INSTRUCTION

The presentation of variation in recent publications such as the “BioCore Guide” (Brownell *et al.*, 2014) and in major textbooks is primarily in the context of genetic mutations or random assortment and recombination in meiosis. In chapters on Mendelian and transmission genetics, variation is often presented as only two options (e.g., white or purple, wrinkled or smooth, dwarf or tall, big *A* or little *a*). In a sense, standard curricula often intentionally simplify or obscure variation in order to highlight more obvious patterns of inheritance. This approach of oversimplifying variation likely makes it even more difficult for students to scale up the connection between genetic variation at the level of mutation and allele to the full spectrum of organismal variation acted on by natural selection and genetic drift. The new *AP Biology Curriculum Framework* (College Board, 2011) does focus on variation at all scales, yet does not make explicit the role of the environment as a modulator of gene expression leading to phenotypic variation, nor does it describe the randomness of genetic drift as an important mechanism for manipulating variation at the population level. We believe that bringing the many levels of variation to the foreground of instruction could aid in the integration of related core concepts. For instance, we might revise the BioCore Guide’s

overarching principle associated with evolution (Brownell *et al.*, 2014) to read “All living organisms vary, yet share a common ancestor” and then allow students to observe, explore, measure, model, and explain variation (e.g., how and to what extent do organisms vary?).

If variation is a threshold concept and is a gateway to mastery, then how might it be foregrounded in the curriculum? In Figure 1, we propose one way to layer different levels of variation in a curriculum hierarchy to emphasize variation at all scales. Although students generally learn early on that the origin of variation is a mutation in DNA, they do not necessarily translate this idea to the impact of such a mutation on phenotypic, population, and species variation. Students’ understanding of variation is further complicated by the role of gene function, selection, and drift and interaction among species as stimulated and modulated by the environment (Figure 1). In addition, because variation is taught in multiple courses, in different contexts, with different vocabulary and different emphases, students may understand the origin of variation in a genetics unit but be unable to apply this understanding to more complex scenarios dealing with variation in ecology and evolution. Focusing on the mechanisms of variation through experiments, modeling, data visualization/analysis, and other means (Lehrer and Schauble, 2004; Lehrer *et al.*, 2007; Duncan and Tseng, 2010; Dauer *et al.*, 2013) may allow students to understand, explain, and connect the small- to large-scale consequences of variation from the level of genotype and phenotype to population and species.

We agree with Baillie *et al.* (2013) that “experiencing variation” should be an explicit goal within the curriculum. Students need instructor guidance to help them notice and make sense of variation within a more “expert” disciplinary framework (Eberbach and Crowley, 2009). Lehrer and Schauble (2004) explain that learning to reason about variation using data leads to inferences that are integrative. As such, this experience is transformative for the learner and “ideally, it results in new (epistemic) worlds” (p. 636). “Variation is ubiquitous, and being able to reason about its qualities comprises a form of literacy with very

broad scope” (p. 676). Furthermore, we believe that *experiencing variation* through scientific practice rather than passively seeing, hearing, or reading about variation is a pathway for integrating and connecting core concepts of genetics and evolution as well as science competencies in a concrete way. This idea is consistent with Duncan and Rivet (2013), who recognized variation as a concept, practice, and epistemology for understanding evolution from a learning progression perspective.

We hypothesize that, in order to cross the threshold that variation may present, students need to observe variation, model it, hypothesize about it, manipulate it, measure it, analyze it, interpret it, and explain it, all with guidance. Figure 2 illustrates an example of such a process: a 4-week project-based unit that integrates genetics and evolution through scientific inquiry, with students applying scientific

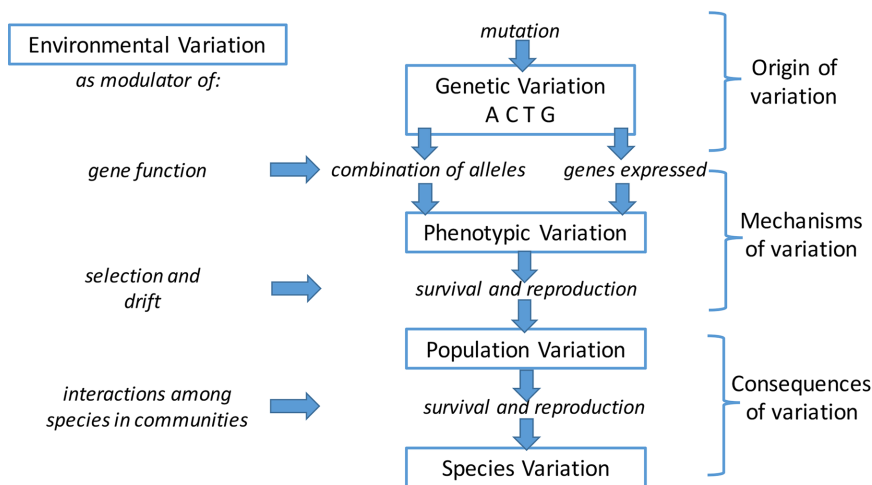


FIGURE 1. Biological variation from genetic, micro/molecular level to phenotypic, population, and species level, all modulated to a greater or lesser extent by environment. Variation can be defined in terms of origin, mechanisms, and consequences.

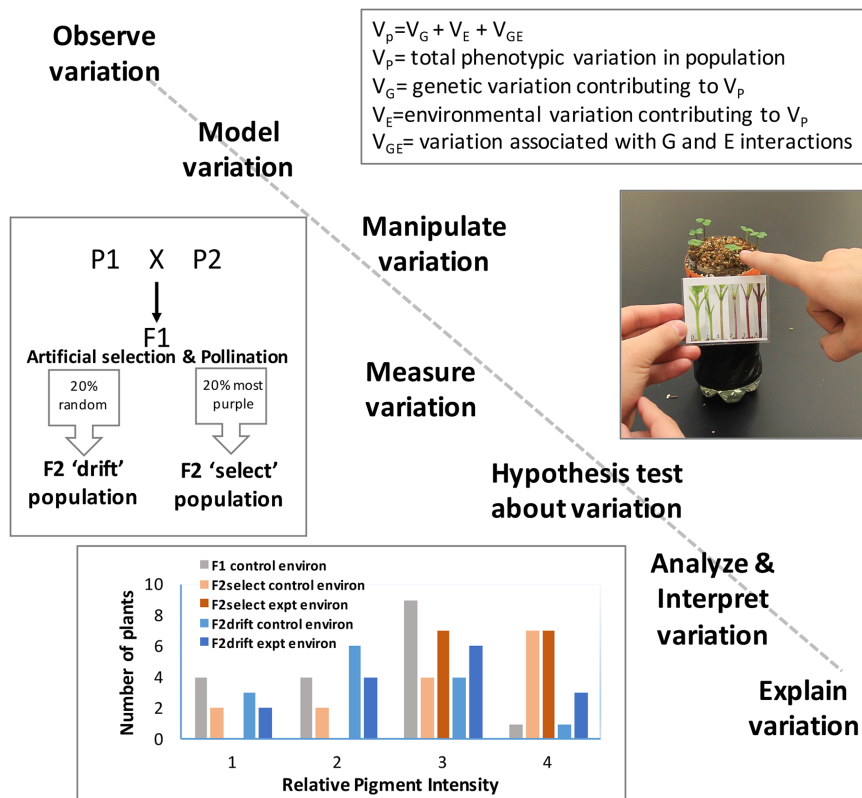


FIGURE 2. Example 4-week curriculum investigating anthocyanin pigment inheritance and expression in *Brassica rapa* Fast Plants, including example student-generated data as histograms with variation represented as distributions (Batzli *et al.*, 2014). This curriculum combines core competencies (AAS, 2011) with the candidate threshold concept of variation and associated concepts outlined in Figure 1.

practices in an investigation of phenotypic variation (Batzli *et al.*, 2014). The unit asks students to examine variation in two genetically distinct populations of plants (*Brassica rapa*) that are exposed to two different environments. The curriculum flow is depicted as a linear progression in Figure 2; however, students' experience and practice with variation is iterative, reflective, often circuitous, and cumulative. In this curriculum, students repeatedly return to troublesome language and challenging concepts, allowing them to pay more attention to the concept of variation. At the start of the unit, students gather initial observations of phenotypic variation in plant stem color. Then they propose a biological rationale or reasons for the variation in the form of a conceptual model and a mathematical model (i.e., $V_p = V_G + V_E + V_{GE}$), leading to hypotheses and an experimental design to test the model, followed by data visualization (e.g., histograms, raw data distributions, box-and-whisker plots, bar chart of means and SDs), data analysis and interpretation, and, finally, a concluding explanation regarding the patterns and variation they observe. This example of a variation-enriched curriculum allows students to experience biological variation through scientific practice.

We argue here that thinking about variation as a threshold concept can inform instructors as they design learning opportunities and experiences for students. We have described one example (Figure 2). There are many other ways to foreground

variation as a threshold concept using various aspects of scientific practice (e.g., students can observe, measure, model, and compare biological variation in human populations, populations of insects, or plants lining campus walkways). Several authors offer other practical approaches for improving instruction and course design using threshold concepts (Cousin, 2006; Land *et al.*, 2006; Burch *et al.*, 2015). These strategies include consideration of “liminal state(s)” that students may need to navigate in their learning and creating opportunities for iterative exposure and application of such potential threshold concepts as variation.

The value of teaching variation is not new, nor is the intentional use of threshold concepts as a heuristic for curriculum development. However, we have offered a new perspective on how to foreground the proposed threshold concept of variation for curriculum development in biology. Baillie *et al.* (2013) contend that when students can use a threshold concept within the conventions of the discipline, they have transformed their understanding. Students who are able to cross the “variation threshold” may have the capability to recognize, apply, model, and manipulate biological variation. Thus, they may be able to design tests for hypotheses to explain biological variation and the essence of the evolutionary process

in a wide range of novel and complex systems (Taylor, 2006).

Presupposing variation as a threshold concept raises several questions: What further empirical studies would confirm variation as a threshold concept? What are the dimensions of variation (biological dimensions, statistical dimensions) or any threshold concept that should be included in curricula? How can we detect whether and when learners have crossed a threshold? With more questions sure to emerge, we feel threshold concepts are an area ripe for dialogue, debate, research, and pedagogical use.

CONCLUSION

In this essay, we engaged in a discussion that presupposes that threshold concepts exist and must be mastered before students can make progress in a discipline. We offered the idea that threshold concepts could provide a bridge that spans concepts and competencies and a means to triangulate frameworks for learning (i.e., learning progressions and *Vision and Change*), thereby integrating often disparate parts of a curriculum. We have found this examination and exploration of threshold concepts to be a powerful exercise, offering a new perspective for curricular design, instruction, and assessment, and for generating hypotheses about our students' learning. Despite the dearth of empirical research on proposed threshold concepts in

biology, we chose to examine the research on students' understanding of variation, a candidate threshold concept. The concept of variation meets many of the proposed criteria for a threshold concept, but definitive empirical research is needed to provide evidence that this concept, in fact, represents a threshold, with consequences to student learning when mastery remains elusive or is unattainable. We hope to inspire researchers and educators to examine threshold concepts in biology, to consider threshold concepts as synergistic with other research areas (e.g., learning progressions), and to ask whether and to what extent highlighting threshold concepts in curriculum development and instruction might lead to improved student learning.

ACKNOWLEDGMENTS

We thank the Introductory Biology Project group for bringing us together and funding our work. This project was supported by a catalytic minigrant awarded to the authors as part of a National Science Foundation Coordination Network grant (RCN UBE: Preparing to Prepare the 21st Century Biology Student, PI Gordon Uno, NSF 0840911). We are grateful for many conversations with colleagues, including Michelle Harris, Karoly Tippets-Russell, and Elise Walck-Shannon, whose insights and questions have been invaluable.

REFERENCES

- American Association for the Advancement of Science (2011). *Vision and Change in Undergraduate Biology Education: A Call to Action*, Washington, DC.
- Anderson DL, Fisher KM, Norman GJ (2002). Development and evaluation of the Conceptual Inventory of Natural Selection. *J Res Sci Teach* 39, 952–978.
- Bahar M, Johnstone AH, Hansell MH (1999). Revisiting learning difficulties in biology. *J Biol Educ* 33, 84–86.
- Baillie C, Bowden JA, Meyer JHF (2013). Threshold capabilities: threshold concepts and knowledge capability linked through variation theory. *High Educ* 65, 227–246.
- Barradell S (2013). The identification of threshold concepts: a review of theoretical complexities and methodological challenges. *High Educ* 65, 265–276.
- Batzli JM, Smith AR, Williams PH, McGee SA, Dósa K, Pfammatter J (2014). Beyond Punnett squares: student word association and explanations of phenotypic variation through an integrative quantitative genetics unit investigating anthocyanin inheritance and expression in *Brassica rapa* Fast Plants. *CBE Life Sci Educ* 13, 410–424.
- Brownell SE, Freeman S, Wenderoth MP, Crowe AJ (2014). BioCore Guide: a tool for interpreting the core concepts of Vision and Change for biology majors. *CBE Life Sci Educ* 13, 200–211.
- Burch GF, Burch JJ, Bradley TP, Heller NA (2015). Identifying and overcoming threshold concepts and conceptions: introducing a conception-focused curriculum to course design. *J Manage Educ* 39, 476–496.
- College Board (2011). *AP Biology Curriculum Framework 2012–2013*, New York.
- Corcoran T, Mosher FA, Rogat A (2009). *Learning Progressions in Science: An Evidence-Based Approach to Reform* (CPRE Research Report# RR-63), New York: Consortium for Policy Research in Education, Center on Continuous Instructional Improvement Teachers College, Columbia University.
- Cousin G (2006). An introduction to threshold concepts. *Planet* 17, 4–5.
- Cousin G (2009). *Researching Learning in Higher Education: An Introduction to Contemporary Methods and Approaches*, New York: Routledge Taylor & Francis.
- Dahlin B (2007). Enriching the theoretical horizons of phenomenography, variation theory and learning studies. *Scand J Educ Res* 51, 327–346.
- Dauer JT, Momsen JL, Bray Speth E, Makohon-Moore SC, Long TM (2013). Analyzing change in students' gene-to-evolution models in college-level introductory biology. *J Res Sci Teach* 50, 639–659.
- Davies P, Mangan J (2007). Threshold concepts and the integration of understanding in economics. *Stud High Educ* 32, 711–726.
- Dobzhansky T (1973). Nothing in biology makes sense except in light of evolution. *Am Biol Teach* 35, 125–129.
- Duncan RG, Reiser BJ (2007). Reasoning across ontologically distinct levels: students' understandings of molecular genetics. *J Res Sci Teach* 44, 938–959.
- Duncan RG, Rivet AE (2013). Science learning progressions. *Science* 339, 396–397.
- Duncan RG, Tseng KA (2010). Designing project-based instruction to foster generative and mechanistic understanding in genetics. *Sci Educ* 95, 21–56.
- Eberbach C, Crowley K (2009). From everyday to scientific observation: how children learn to observe the biologist's world. *Rev Educ Res* 79, 39–68.
- Garvin-Doxas K, Klymkowsky MW (2008). Understanding randomness and its impact on student learning: lessons learned from building the Biology Concept Inventory (BCI). *CBE Life Sci Educ* 7, 227–233.
- Gregory TR, Ellis CAJ (2009). Conceptions of evolution among science graduate students. *BioScience* 59, 792–799.
- Hallgrímsson B, Hall BK (2005). *Variation: A Central Concept in Biology*, London: Elsevier Academic.
- Hartley L, Doherty JH, Harris C, Moore JC, Berkowitz AR, Anderson CW (2014). *Learning Progression Framework and Assessments For Community Ecology*, Pittsburgh, PA: National Association for Research in Science Teaching.
- Lin H, Zhan L, Anderson CW (2013). Developing a fine-grained learning progression framework for carbon-transforming processes. *Int J Sci Educ* 35, 1663–1697.
- Kinchin IM (2010). Solving Cordelia's dilemma: threshold concepts within a punctuated model of learning. *J Biol Educ* 44, 53–57.
- Land R, Cousin G, Meyer JHF, Davies P (2006). Implications of threshold concepts for course design and evaluation. In: *Overcoming Barriers to Student Understanding: Threshold Concepts and Troublesome Knowledge*, ed. JHF Meyer and R Land, London: Routledge, 195–206.
- Lehrer R, Kim M, Schauble L (2007). Supporting the development of conceptions of statistics by engaging students in measuring and modeling variability. *Int J Comput Math Learn* 12, 195–216.
- Lehrer R, Schauble L (2004). Modeling natural variation through distribution. *Am Educ Res J* 41, 635–679.
- Loertcher J, Green D, Lewis JE, Lin S, Minderhout V (2014). Identification of threshold concepts for biochemistry. *CBE Life Sci Educ* 13, 516–528.
- Meyer JHF, Land R (2003). *Threshold Concepts and Troublesome Knowledge: Linkages to Ways of Thinking and Practicing within the Disciplines* (Occasional Report 4), Edinburgh, UK: Enhancing Teaching-Learning Environments in Undergraduate Courses Project, Higher and Community Education, School of Education, University of Edinburgh.
- Meyer JHF, Land R, Davies P (2006). Implications of threshold concepts for course design and evaluation. In: *Overcoming Barriers to Student Understanding: Threshold Concepts and Troublesome Knowledge*, ed. JHF Meyer and R Land, Abingdon, UK: Routledge.
- Mohan L, Chen J, Anderson CW (2009). Developing a multi-year learning progression for carbon cycling in socio-ecological systems. *J Res Sci Teach* 46, 675–698.
- National Research Council (2007). *Taking Science to School: Learning and Teaching Science in Grade K–8*, Washington, DC: National Academies Press.
- Nehm RH, Reilly L (2007). Biology majors' knowledge and misconceptions of natural selection. *BioScience* 57, 263–272.
- Posner G, Strike K, Hewson P, Gertzog W (1982). Accommodation of scientific conceptions: toward a theory of conceptual change. *Sci Educ* 66, 211–227.

- Price RM, Andrews T, McElhinny TL, Mead LS, Abraham JK, Thanukos A, Perez KE (2013). The Genetics Drift Inventory: a tool for measuring what advanced undergraduates have mastered about genetic drift. *CBE Life Sci Educ* 13, 65–75.
- Quintan KM, Male S, Baillie C, Stamboulis A, Fill J, Jaffer Z (2013). Methodological challenges in researching threshold concepts: a comparative analysis of three projects. *High Educ* 66, 585–601.
- Ross PM, Taylor CE, Hughes C, Kofod M, Whitaker N, Lutze-Mann L, Tzioumis V (2010). Threshold concepts: challenging the way we think, teach and learn in biology. In: *Threshold Concepts and Transformational Learning*, ed. JHF Meyer, R Land, and C Baillie, Rotterdam, Netherlands: Sense Publishers, 165–177.
- Rountree J, Rountree N (2009). Issues regarding threshold concepts in computer science. *Proceedings of the Eleventh Australasian Conference on Computing Education*, vol. 95, Sydney, NSW: Australian Computer Society, 139–146.
- Rowbottom DP (2007). Demystifying threshold concepts. *J Phil Educ* 41, 263–270.
- Shtulman A, Schultz L (2008). The relation between essentialist beliefs and evolutionary reasoning. *Cogn Sci* 32, 1049–1062.
- Smith MU (2010a). Current status of research in teaching and learning evolution. I. Philosophical/epistemological issues. *Sci Educ* 19, 523–538.
- Smith MU (2010b). Current status of research in teaching and learning evolution. II. Pedagogical issues. *Sci Educ* 19, 539–571.
- Taylor C (2006). Threshold concepts in biology: do they fit the definition? In: *Overcoming Barriers to Student Understanding: Threshold Concepts and Troublesome Knowledge*, ed. JHF Meyer and R Land, Abingdon, UK: Routledge, 87–99.
- Taylor C (2008). Threshold concepts, troublesome knowledge and ways of thinking and practicing. In: *Threshold Concepts within the Disciplines*, ed. R Land, JHF Meyer, and J Smith, Rotterdam, Netherlands: Sense Publishers, 185–197.
- White JS, Maskiewicz AC (2014). Understanding cellular respiration in terms of matter and energy within ecosystems. *Am Biol Teach* 76, 408–414.