Science education

As biological research increasingly relies on and requires the integration of different concepts and methods, educators face new challenges in training students to become skilled practitioners and knowledgeable consumers of the "New Biology" (NRC, 2009). The 2011 Vision and Change in Undergraduate Biology Education report (V&C ref), developed collaboratively by the NSF, AAAS, HHMI, and NIH, identifies five core concepts and six core competencies that provide a framework for improving undergraduate biology education. The integrative nature and diversity of research approaches employed in Evo-Devo, combined with the subject matter itself, make it perfectly suited for achieving these goals (Love 2013, 2013). Here, we illustrate how principles and findings from Evo-Devo can be used to teach three core concepts and three core competencies identified in this report.

Core Concept: Evolution

Development is the product of evolution and evolutionary change occurs in the context of developmental systems, yet evolution and development are usually taught separately. Connections between these two fields are often relegated to the end of a course or textbook. Incorporating Evo-Devo more fully into the standard biology curriculum will improve student understanding of evolutionary processes responsible for the diversity of organisms found in nature. Students who learn that evolution results from mutations generating phenotypic diversity and selection preferentially retaining the fittest genotypes can mistakenly think that all phenotypic possibilities have been explored and that species are optimally adapted to their surroundings. Evo-Devo challenges this misconception by emphasizing the "arrival of the fittest" (Fontana & Buss) and showing how the existing developmental program can bias the range of phenotypes generated by new mutations (Brakefield). A rich collection of case studies now exists demonstrating how phenotypic diversity has resulted from the duplication, rearrangement, and redeployment of existing developmental processes. Many of these studies involve species and traits that are inherently interesting to students (e.g., mammalian flight).

Core Concept: Structure and Function

Evo-Devo aims to understand how changes in DNA sequence affecting gene expression and/or protein function ultimately lead to novel phenotypes. Studies of natural variation within a species or divergence between species complement developmental biology studies of mutations isolated in the laboratory. Evo-Devo also fills a critical gap in linkage-mapping and association studies by showing how associated genetic changes alter development to produce phenotypic variation. For example, many examples of regulatory changes underlying biodiversity have been described that can be used to illustrate the power of regulatory changes to alter phenotypes in other (e.g., medical) contexts (Wray cis reg review). Case studies from Evo-Devo remind students that structure-function relationships are often deeply conserved and shared among diverse organisms (e.g., Pax6 in eye development, jaw morphology in birds and fish, MADS box genes in land plants), but also exhibit variation even within closely related species or populations (e.g., endo16, Rausher; Kijimoto et al. 2012).

Core Concept: Systems

Evo-devo offers opportunities to teach systems biology—"quantitative understanding of complex biological processes through an elucidation of the dynamic interactions among components of a system at multiple functional scales" (V&C ref)—by connecting genetic changes with their (a) molecular, developmental and phenotypic consequences, (b) effects on fitness in particular ecological contexts, and (c) longer-term evolutionary fate. A number of "metamodels" (Kopp) have been dissected in sufficient detail to facilitate this type of teaching strategy. For example, the genetic, molecular, and developmental mechanisms underlying divergent pigmentation have been elucidated in flies, butterflies, mice, fish, and plants (animal review, REFs), as well as the ecological interactions that cause changes in pigmentation to affect fitness (REFs).

Core Competency: Ability to use modeling and simulation

Computational models and simulations allow researchers to represent and explore complex processes by integrating findings from multiple studies, allowing the impact of different parameters to be explored *in silico*. In Evo-Devo, computational models of developmental processes have been used to test evolutionary hypotheses and predict morphological consequences of genomic changes to regulatory networks (teeth, von Dossow). For example, a model of inflorescence development in plants suggested that certain phenotypes are likely not found in nature because of developmental constraints and predicted associations between inflorescence shape, life history, and environmental conditions that are indeed found among natural populations (Prusinkiewicz). Students can learn to manipulate these models in computer labs and make their own predictions about development and evolution, similar to the pedagogical use of models from population genetics and phylogenetics.

Core Competency: Ability to tap into the interdisciplinary nature of science

Evo-Devo began with the integration of evolution and development as its core aim and put special emphasis on comparative studies of development. Contemporary Evo-Devo retains this perspective, but also incorporates theory, methods, and data from fields such as paleontology (Shubin review), population genetics (sticklebacks), neurobiology (burrowing behavior), quantitative genetics (sunflowers, directional selection), molecular biology (single aa change switches male to female in flower), molecular ecology (salt tolerance in plants), phylogenetics (example) and genomics (gene expression in natural populations). Most college biology courses focus on a single discipline, leaving students to integrate information from different approaches on their own (if at all). In contrast, Evo-Devo is inherently interdisciplinary; it demonstrates how information can be shared and interpreted across disciplinary boundaries in a variety of ways. For example, interdisciplinarity can be taught by focusing on a single meta-model (Kopp) and examining it from multiple perspectives. For example, classical and quantitative genetics can be used identify the genetic changes underlying a divergent phenotype, molecular and experimental methods of developmental biology can be used to determine how the identified genetic changes impact the phenotype, and ecological and evolutionary theory can be used to examine the impact of the phenotypic change on the species of interest.

Core Competency: Ability to communicate and collaborate with other disciplines

The interdisciplinary nature of Evo-Devo naturally fosters the ability to communicate and collaborate. This core competency can be taught by having students work in teams to explore the evolution and development of a particular trait. For example, each student can be assigned a different role in a hypothetical Evo-Devo research team (geneticist, developmental biologist, population geneticist, ecologist, paleontologist, or phylogeneticist) and asked to find information from their disciplinary vantage point, working with their peers to assess how the different types of information fit together. Such an activity would reflect the reality of Evo-Devo research in which interdisciplinary projects are advanced despite individual researchers having primary training in only one or two disciplines. Students would quickly learn that making the most of everyone's individual skills and perspectives requires the ability to communicate clearly by translating key terminology into new domains and finding ways to explain important technical issues that are often overlooked when traversing disciplinary boundaries.

In summary, Evo-Devo provides an outstanding platform for teaching biology because it integrates multiple core concepts and provides opportunities to develop core competencies. It also shows how escaping programmatic boundaries and integrating data from diverse disciplines results in novel and transformative discoveries.