

From deep roots to new blooms: The ever-growing field of evo–devo across land plants

1 | INTRODUCTION

At its core, the field of evolutionary developmental biology aims to understand how morphological innovations arise. Do new structures require new toolkits or can they be made by tweaking existing ones (Brakefield, 2011; Della Pina et al., 2014)? Are certain loci or types of mutations more likely to contribute to phenotypic evolution (Sobel & Streisfeld, 2013; Stern & Orgogozo, 2008)? To what degree do convergently evolved traits rely on the same underlying mechanisms and can we predict when such molecular and developmental convergence is likely to occur (Martin & Orgogozo, 2013)? Addressing these questions requires a comparative approach, from the studies of sister taxa where trait divergence has recently occurred to comparisons across entire phyla to understand features that only vary at the deepest scales.

Botany has a long history of comparative developmental research (Endress et al., 2000), and placing this line of research in the context of the fossil record has built an increasingly clear picture of major innovations spread across the plant phylogeny (Harrison, 2017; Rothwell et al., 2014). One perhaps surprising theme that has emerged from our growing understanding of plant evolutionary history is the degree to which major innovations have evolved multiple times. For example, leaves and roots independently evolved in the lycophytes (club mosses and allies) and the euphyllophytes (ferns and seed plants) (Spencer et al., 2021). Similarly, colorful fleshy structures surrounding seeds to enhance dispersal have evolved in both gymnosperms and in angiosperms (Di Stilio & Ickert-Bond, 2021; Figure 1). These striking instances of convergent evolution raise the question of whether these repeated innovations drew from conserved mechanisms, present in the common ancestors of these lineages hundreds of millions of years in the past.

Probing the possibility of such deep homology (Shubin et al., 2009) has become an important focus for plant evo–devo research and led to significant efforts to develop genomic resources and molecular tools across diverse plant lineages. As study organisms, plants present some exceptional benefits, such as the ease of clonal

propagation, the ability to self-fertilize (in some taxa), the large numbers of offspring (in some taxa), and the wide crossability among species, often spanning different genera. Nevertheless, studying plant diversity beyond *Arabidopsis* frequently means overcoming a range of technical and computational challenges, from developing species-specific tissue culture and regeneration for transformation to assembling large, repetitive and/or highly heterozygous genomes. Indeed, the cells of the monocot *Paris japonica* are stuffed with the largest known eukaryotic genome, a 149 Gb goliath that is roughly 50 times the size of the human genome (Pellicer et al., 2010).

Despite these challenges, comparative research in plant developmental biology promises new insights into a range of longstanding areas of interest in evo–devo, including how pathways arise and become rewired over evolutionary time as new structures emerge, and how development is evolutionarily fine-tuned as species diverge. Discoveries from plant evo–devo not only illuminate these basic questions but contribute to important advances in applied research in agriculture, horticulture and even medicine (Davies et al., 2012; Doebley et al., 2006; Gershlak et al., 2017; Lemmon et al., 2018). This special issue highlights recent advances emerging from taxa across the plant tree of life as well as the prospects for new discoveries in the years to come.

2 | HOW DOES SIGNALING EVOLVE IN CONJUNCTION WITH MORPHOLOGICAL EVOLUTION?

Development requires shared signals across an organism to coordinate growth and expansion and to integrate information from the environment. This question of how to coordinate signals across the organism over time is particularly important in plants given that their development is modular, typically indeterminate, and lacking the capacity for cell migration. For example, multiple environmental cues feed into the transition from vegetative growth to reproduction, and this decision point

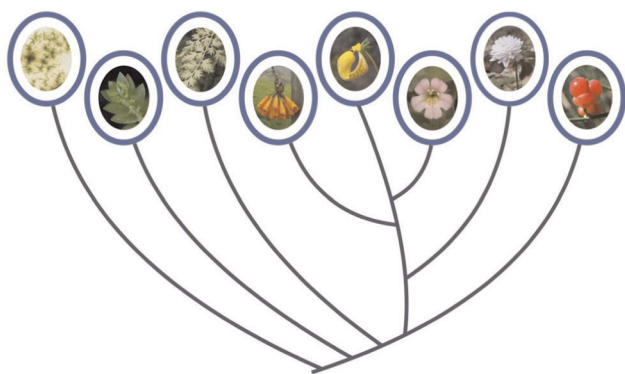


FIGURE 1 Study systems across land plants investigated in this special issue. Images left to right: moss *Physcomitrium patens* (Hedw.) Mitt.; lycophyte *Selaginella kraussiana* (Kunze) A. Braun; fern *Lygodium japonicum* (Thunb.) Sw.; trailing lily *Bomarea multiflora* (L.f.) Mirb.; slipper flower *Calceolaria polyrhiza* Cav.; Parish's monkeyflower *Erythranthe parishii* (Greene) G.L. Nesom & N.S. Fraga (or *Mimulus parishii* Greene); rue-anemone *Thalictrum thalictroides* (L.) A. J. Eames & B. Boivin, double flower mutant in the wild; and fleshy propagules of the gymnosperm *Ephedra distachya* subsp. *helvetica* (C.A. Mey.) Asch. & Graebn. Photos by L. Moody, V. Spencer, E. Guinther, F. Alzate-Guarín, A. A. Cocucci, Y. Yuan, D. Walters, and E. Zippel, respectively

must be translated across the plant to initiate flower development across the (often many) apical meristems (Andres & Coupland, 2012; Blackman, 2017). As in animal systems, hormonal signaling is key in orchestrating growth and developmental transitions, and studies across plants have revealed how widely shared many of these signaling systems are. For example, Jaeger and Moody (2021) describe how auxin signaling directs the remodeling of the actin cytoskeleton and in turn cell expansion and division associated with the transition from a single growing tip into three-dimensional branching shoots in the moss *Physcomitrium patens*. The genetic and hormonal mechanisms regulating tip growth in *P. patens* are deeply conserved, with similar systems controlling root hair formation and pollen tube growth in flowering plants as well as hyphal expansion in fungi (reviewed in Jaeger & Moody, 2021).

Despite their position at the very core of organismal function, hormone-based signaling systems have evolved in conjunction with the evolution of new body plans and life histories. For instance, over the course of evolution, gibberellins (GAs) have become key hormonal regulators of plant growth responses, from seed germination to stem elongation to the induction of flowering. Yet while GAs were not produced by early land plants, the DELLA proteins that regulate many responses to GA were already present and have their own a highly dynamic

evolutionary history (Phokas & Coates, 2021). Comparative studies of gene family evolution and DELLA-mediated signaling across land plants (including bryophytes, lycophytes, ferns, and seed plants) point to multiple functional transitions, with members of this gene family being newly deployed as targeted growth repressors in particular organs or at specific developmental time points. Indeed, Phokas and Coates (2021) suggest that the DELLA signaling pathway was recruited into regulating GA responses, possibly exploiting a pre-existing propensity for interaction between GA and the DELLA n-terminal domain, much in the way that the ancestral mineralocorticoid receptor presented affinity for aldosterone long before the hormone became involved in signaling in vertebrates (Bridgham et al., 2006).

3 | HOW DO SHARED TOOLKITS CONTRIBUTE TO MORPHOLOGICAL INNOVATION AS WELL AS REPEATED EVOLUTION?

The theme of recruitment and modification of shared molecular toolkits during plant diversification extends well beyond signaling pathways. For example, many lineages of plants have independently evolved underground storage organs like the leaf-derived bulbs of onions or the stem tubers of potatoes. Even when formed from distinct organ precursors, similar molecular mechanisms may guide their development (Tribble et al., 2021). The independent evolution of roots in lycophytes and euphyllophytes offers another compelling example at an even wider taxonomic scale. The involvement of similar suites of genes in these developmentally different but functionally similar structures suggests either convergent recruitment of particular developmental pathways or conservation of an ancestral root development program throughout the vascular plant phylogeny (Spencer et al., 2021).

In addition to highlighting when convergent evolution has leveraged similar molecular toolkits, expanding our focus to additional traits and lineages has provided opportunities to learn how modification and expansion of these toolkits can lead to new functions and structures. As work by Martinez-Gomez et al. (2021) shows, shuffled regulatory patterns of the floral MADS-box genes (components of the classic ABC model of floral organ development) underlie the origin of spontaneous homeotic mutants in the rue anemone *Thalictrum thalictroides* with entire floral whorls gained and lost. The history of these MADS-box genes is equally dynamic in the lycophytes, which lack flowers and reproduce by the

production of spores in cone-like strobili. Ambrose et al. (2021) document two rounds of duplication within the lycophytes, with the homologs showing different expression patterns suggestive of specialization for different developmental functions.

4 | HOW DOES DEVELOPMENTAL VARIATION AT THE MICROEVOLUTIONARY SCALE RELATE TO DIFFERENCES AT THE SPECIES LEVEL OR HIGHER?

An additional long-standing focus in evo-devo is the connection between processes that govern the origin and sorting of variation at the population level with those that yield macroevolutionary scale divergence and innovation. Fundamentally, the goal of research in this area is to understand the genetic and developmental basis for morphological variation within and among populations, reveal phenomena that act as constraints or promote evolvability, and ultimately build an integrative understanding for how these all yield divergence at the species level over time (Stern, 2011). One topic that has emerged as particularly germane to this question is heterochrony, namely, changes in the timing of developmental processes. Small shifts in rates or duration of cell division and expansion can lead to large differences in organismal phenotype and act as sources of variation upon which selection can act. For instance, Strelin et al. (2021) report how shifts in growth trajectories across populations of the slipper flower *Calceolaria polyrhiza* have led to differences in shape that are linked with differences in pollinator associations.


Over deeper time, these developmental dynamics can lead to species-level divergence, such as in the florally diverse monkeyflowers of the *Mimulus* section *Erythranthe*. Gurung et al. (2021) demonstrate that the small flowers of the self-pollinating species *M. parishii* result from a truncation of development with anthesis (maturation) occurring after only half the number of days as in its bee-pollinated relative *M. lewisii*. Meanwhile, the elongated corolla tubes of the hummingbird-pollinated *M. verbenaceus* do not arise as a consequence of faster growth but instead due to a longer time to anthesis combined with a sharp uptick in elongation late in development (Gurung et al., 2021). A clear next step in this study program will be to identify the underlying genetic changes and investigate how they influence the timing of floral organ development in conjunction with known hormonal signals and upstream pathways (Chandler, 2011).

5 | LOOKING AHEAD

The tremendous and continued growth of plant evo-devo research has built upon a strong phylogenetic framework, allowing us to identify gaps in our understanding, target our taxon selection to the questions at hand, and place our findings in a broad evolutionary context. The findings presented in this special issue reinforce our understanding that the story of evolution is one of diversification, not a directional march of progress (Baum et al., 2005; McDaniel, 2021). Pathways inherited from ancestors have been co-opted and modified for new and diverse functions countless times across plants, just as new gene networks and interactions have continued to appear through the course of evolution across all lineages. By expanding the model organisms for evo-devo research, plant biologists have brought greater resolution to key ancestral states in plant evolutionary history and begun to elucidate the series of steps responsible for major transitions, such as the evolution of multicellularity and heterospory. Moving forward, continued focus on selecting study taxa for both their character diversity and phylogenetic position (Di Stilio & Ickert-Bond, 2021) will maximize our progress towards a broad understanding of the mechanistic basis for morphological innovation.

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