



## SYMPOSIUM

# Plant Evolutionary Ecology in the Age of the Extended Evolutionary Synthesis

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**Synopsis** Plant ecology is increasingly turning to evolutionary questions, just as evolutionary biology pushes out of the strictures of the Modern Synthesis into what some regard as an “Extended Evolutionary Synthesis.” As plant ecology becomes increasingly evolutionary, it is essential to ask how aspects of the Extended Synthesis might impinge on plant ecological theory and practice. I examine the contribution of plant evolutionary ecology to niche construction theory, as well as the potential for developmental systems theory and genes-as-followers adaptive evolution, all important post-Modern Synthesis themes, in providing novel perspectives for plant evolutionary ecology. I also examine ways that overcoming dichotomies such as “genetic vs. plastic” and “constraint vs. adaptation” provide fertile opportunities for plant evolutionary ecologists. Along the same lines, outgrowing vague concepts such as “stress” and replacing them with more precise terminology in all cases provides vastly increased causal clarity. As a result, the synthetic path that plant ecologists are blazing, becoming more evolutionary every year, bodes extremely well for the field, with vast potential for expansion into important scientific territory.

## Introduction

Over 15 years ago, [Ackerly and Monson \(2003\)](#) referred to the vast potential for rigorous evolutionary thinking to produce a conceptually robust evolutionary plant ecology as the “sleeping giant.” They envisioned a plant ecology built solidly on evolutionary theory, citing decades of thinking regarding selection, adaptation, and the factors that limit or direct these processes, as well as methods such as optimality modeling using basic biophysics to predict phenotypes that should be favored by selection ([Vincent and Brown 2005](#); [Olson and Arroyo-Santos 2015](#)). In many respects the giant has without a doubt risen, bearing out Ackerly and Monson’s predictions of promise. Plant evolutionary ecological studies in terms of the phylogenetic comparative method have burgeoned ([Anderegg et al. 2018](#); [Zanne et al. 2018](#)). Optimality models of plant function are more abundant and sophisticated than ever ([Savage et al. 2010](#); [Banavar et al. 2013](#); [Christoffersen et al. 2016](#)). Discussion of key theory and ideas is rapidly shedding limiting baggage of old frameworks and expanding into novel, more biologically accurate,

territory ([Kraft et al. 2015](#); [Baldwin 2017](#); [Cadotte and Tucker 2017](#); [Courchamp et al. 2017](#); [Körner and Hiltbrunner 2018](#)). The giant is undeniably awake, and in some respects has already had a cup of coffee and has headed out the door.

But even as plant ecology converges on evolutionary biology, evolutionary biology itself is a moving target. Evolutionary biology is surging beyond the strictures of the Modern Synthesis (MS), the early 20th-century effort to extrapolate all evolutionary patterns to standard population-level processes of mutation, drift, and selection ([Pigliucci 2008](#)). Many biologists in the decades following the *Origin of Species* regarded natural selection to be an unlikely or uncommon cause of evolution, largely because the notions of inheritance of the day predicted change even in the absence of selection ([Bowler 1983](#)). The rediscovery of Mendel’s laws in 1900 and the publication of the Hardy–Weinberg principle in 1908 showed that allele frequencies should remain constant across generations in the absence of selection or drift. Through the 1930s, these insights powered the founding of modern population genetics, which

models evolution as change in allele frequencies largely as the result of selection, mutation, and drift (Jablonka and Lamb 2005; Pigliucci and Müller 2010). Biologists found that they could construct plausible explanations for many evolutionary patterns, from adaptation in local populations to morphological changes in the fossil record, by extrapolating from basic population genetic processes (Simpson 1953; Mayr 1982). This extrapolation was dubbed the Modern Synthesis in 1942 (Huxley 1942) and is the framework against which all evolutionary biology has been conducted, and against which it has often reacted, ever since.

Since the founding of the MS, empirical data have butted against its limitations. Where the MS viewed genes as somehow being the ultimate causes of phenotypes, and meaningfully separate from them, modern genetics and systems biology are clearly showing genes to be necessary but not sufficient for inheritance (Jablonka and Lamb 2005; Pigliucci 2010; Griffiths and Stotz 2013). Decades of data on phenotypic plasticity and genetic assimilation seriously undermine the notion that mutation is the sole driver of variation that selection can act on in populations, and instead phenotypic plasticity provides an abundant source of adaptively-directed variation (West-Eberhard 2003). Foundational assumptions such as the separability of ontogeny and evolution, genotype and phenotype, organism and environment, the level of biological organization at which selection can act, and even the definition of evolution itself, are all being compellingly reexamined (Table 1; Odling-Smee et al. 2003; Jablonka and Lamb 2005; Blumberg 2010; Caporael et al. 2014; Fábregas-Tejeda and Vergara-Silva 2018). Many biologists consider these considerations to go so far beyond the restricted view of the MS that they denote a new view in evolutionary biology, the Extended Evolutionary Synthesis (EES) (Pigliucci and Müller 2010; Laland et al. 2015). EES themes include the importance of ontogenetic biases in directing the variation available for selection to act on (often referred to under the rubric of “evolvability”), emphasis on the mutual shaping of organism and environment, a widening of the study of heritability beyond just genes, emphasis on the importance of phenotypic plasticity as a source of evolutionarily relevant variation, and other themes. Many scientists suggest that the EES and related ideas are not qualitatively different and just the natural growth of the MS (Coyne 2009; Minelli 2010; Charlesworth et al. 2017; Futuyma 2017), but whatever its views are called, it is clear that today’s evolutionary biology gives many themes much

more emphasis today than it did even just 20 years ago.

As the plant evolutionary ecological giant makes ever more confident strides in its wakefulness, it is important to ask where it is headed as it marches into the changing landscape of evolutionary biology. Much has changed since Ackerly and Monson (2003), whose essay was firmly grounded in a MS perspective. Yet plant evolutionary ecologists are responsible for foundational studies that provide paradigm illustrations of aspects of the EES, and the potential of plant evolutionary ecology to contribute powerfully to debates regarding the EES remains vast. In other cases, the giant remains decidedly asleep, with evolutionary thinking having far surpassed current thinking in plant evolutionary ecology. Here, I briefly examine examples of both of these aspects, areas in which plant evolutionary ecology has contributed to, or has the potential to contribute to, foundational aspects of the EES. I also highlight conceptual refinements in evolutionary biology where plant evolutionary ecology tends to lag behind, and where a little shaking would give the giant welcome direction.

## Outgrowing limiting concepts

One of the many compelling aspects of current evolutionary thought is the challenging of restrictive conceptual frameworks. Some of the most conspicuous of these revisions include the rejection of genes as the sole locus of inheritance, and to some, even the conventional notion of “gene” as an entity in nature that can be meaningfully regarded as a cause of phenotypes (West-Eberhard 2003; Stotz et al. 2004; Jablonka and Lamb 2005; Buchanan et al. 2009; Blumberg 2010). Another includes the view of existing organismal structures as “scaffolds” on which ontogeny builds. This view extends to DNA, which, far from a neutral bearer of “information” that could just as easily be in a different form, in fact is a physical template on which other molecules are crucially built (Caporael et al. 2014). Other important avenues involve challenging key conceptual dichotomies (e.g., that differences between individuals can be ascribed to “genetics” vs. phenotypic plasticity or that trait distributions can be explained by adaptation vs. constraint) and increasingly sophisticated treatment of the metaphors that fill ecology and evolutionary biology (e.g., niche, filtering, competition, and stress) (de Lorenzo 2011; Olson 2012, 2019; Taylor and Dewsbury 2018; Olson et al. 2019). I touch on a just a few of these developments here,

**Table 1** Examples of contrasts in some views of the MS and the EES and related post-MS evolutionary theory

Precept	Modern synthesis	Extended synthesis
The unit of inheritance	Gene	Developmental system (DNA plus the minimal set of developmental components necessary for constructing a new individual that resembles the ancestral phenotype)
The cause of change between generations	Selection, drift	Selection, drift, developmental bias/developmentally inaccessible morphospace, contingency
The definition of evolution	Change in allele frequency	Change in developmental systems
The source of evolutionarily relevant variation within populations	Mutation	Genetic mutations, epigenetic shifts, plasticity-first evolution, developmental bias
The level at which natural selection acts	Between individuals within populations	Evolutionary individuals and populations can be at many hierarchical levels, both below (e.g., cells within individuals) and above (e.g., species within clades) the traditional level
Differences between micro- and macro-evolution	Macroevolution is simply repeated rounds of microevolution extrapolated to large time scales	Macroevolution (change in trait frequencies given differences in tendency to persist in geological time or to speciate between species) is qualitatively distinct and not reducible to microevolution
Explanation of morphological discontinuities between taxa	Adaptation to differing selective contexts; morphological discontinuities diagnose environmental discontinuities	Adaptation to differing conditions, developmental bias/impossibility
Directionality of the variation exposed to selection	Mutations are random with respect to phenotypic effect	In plasticity-first evolution, change is directedly adaptive
Timing and genomic location of mutation	Random with respect to the relevant selection pressure	Mutation rate or location in the genome can be higher or lower in ways that appear adaptive
Ontogeny versus evolution dichotomy	Ontogeny is the mere unfolding of the genetic program shaped by evolution; an irrelevant black box	The crucial construction of a new individual in ways that can profoundly influence the variation exposed to selection, and therefore a necessary object of study

ones particularly relevant to plant evolutionary ecology.

### Variation due to (mere) phenotypic plasticity or (real) genetic variation

Plant evolutionary ecologists often ask whether variation is “genetic” or “plastic” (Franks et al. 2014; Andereg 2015), a question that often implies that the former represents true difference and the latter not. Most of the time, on closer inspection, these authors are actually referring to the amplitude of phenotypic plasticity. Phenotypic plasticity is the capacity of a single developmental system or genotype to produce a range of different morphological or physiological configurations in different environments. This capacity is adaptive, i.e., favored by selection, with the configuration produced in a given environment being associated with higher fitness than the other configurations that the developmental system can produce (Ehrenreich and Pfennig 2016). It is very important to recognize that phenotypic plasticity is an adaptive phenomenon for two reasons. First, it shows that the plasticity–genetic

dichotomy does not make sense from the outset. To the extent that natural selection involves genetic inheritance, then phenotypic plasticity as an adaptive phenomenon necessarily is “genetic.” Differing patterns of gene expression are always involved in the production of differing plastic configurations, too, making phenotypic plasticity “genetic” in this ontogenetic sense as well (Pigliucci 2005). The second reason for recognizing phenotypic plasticity as adaptive is that it permits distinguishing between plasticity and pathology. There are many changes associated with differing environmental conditions. For example, smoking is associated with greater risk of heart attacks, exposure to radiation is associated with cancer, and low caloric intake in youth is associated with stunting. Unless phenotypic plasticity is defined as adaptive, there is no way to say that these examples, or for that matter death from strychnine, are not phenotypically plastic responses to differing environmental conditions. Because phenotypic plasticity always involves genetic factors, the plastic–genetic response cannot be what fundamentally interests plant evolutionary ecologists.

On careful inspection, plant evolutionary ecologists are actually referring to the amplitude of phenotypic plasticity responses. All traits of interest to plant ecologists are subject to at least some plastic variation in size, metabolism, or other attributes with environment. When ranges of phenotypic plasticity are wide within species and the differences across species are relatively low, then the differences are said to be “plastic.” When phenotypic plasticity ranges are narrow and variation across species is wide, the differences are said to be “genetic” (Montes-Cartas et al. 2017). It is important to recognize when this distinction is important and when it is not. In some cases, plant evolutionary ecologists want to know whether ranges of phenotypic plasticity are sufficiently wide as to be plausibly included within climate change scenarios. That is, does the climate range that the individuals of a given species have a plastic response to fall within a given projected climate change scenario? Alternatively, they might wish to know whether standing heritable variation across individuals within populations provides raw material for an intergenerational response to the novel selective conditions imposed by changing climates (Chevin et al. 2010). Neither of these important questions is helped by the false “genetic–plastic” dichotomy.

In addition to these considerations, even if it were possible to make a meaningful plastic–genetic distinction, for many explanations it is not really an important player in accounting for biological patterns. Take as an example the explanation of a gradient in size of leaves, from small leaves in the desert to large leaves in tall rainforest. If this pattern was observed between species, each species with a fixed leaf size, i.e., “genetic” differences, how would we explain this gradient in size? It would be possible to construct an explanation in terms of energy/heat budgets, boundary layer thickness, stomatal conductance, photosynthetic rates, and carbon fixation per carbon investment. This explanation would appeal to these biophysical considerations to show why in the desert individuals with small leaves would have greater fitness than those with large leaves, and vice-versa for the rainforest. Now imagine clones of a single individual planted across the desert-rainforest gradient with the same gradient in leaf area, i.e., now the same morphology–environment range would be chalked up to phenotypic plasticity. To explain why the clones produce leaves of different sizes in different environments, we would appeal to energy/heat budgets, boundary layer thickness, stomatal conductance, photosynthetic rates, and carbon fixation per carbon investment, that is, exactly the

same considerations as in the interspecific case. For purposes of biophysical explanations of why certain variants should be favored over others, the plastic/genetic distinction is entirely irrelevant. Distinguishing between situations when questions of phenotypic plasticity are important or not will provide important direction for empirical work.

### Constraint versus adaptation

Often when confronted with a striking pattern of trait covariation, such as the remarkable tendency for leaf lifespan to predict leaf mass per unit area across species (Wright et al. 2004), plant evolutionary ecologists often ask whether these patterns are caused by “adaptation or constraint” (e.g., Marquardt and Pennings 2011). Like phenotypic plasticity versus genetics, this dichotomy is also one that is difficult to defend biologically, but paradoxically the “constraint or adaptation?” question is an essential first step for investigating the empirical causes of trait distributions. It is paradoxical because, for all its empirical utility, there are three reasons to reject the reality of this dichotomy and indeed to avoid the use of the term “constraint” altogether in favor of more precise vocabulary. The first is that “constraint” is a vague term that does not designate a specific phenomenon in nature (Pigliucci 2007). There are many conceptions of “constraint,” such as ontogenetic, phylogenetic, environmental, allometric, genetic (including quantitative genetic), or even selective constraints. As a result, more often than not, speaking in terms of “constraint” without careful specification of what is meant by the term just leads to scientists talking past one another. In addition, both “constraint” (by any definition) and selection are involved in the generation of any given pattern of trait distribution. As a result, there is no situation in which speaking in blanket terms about “constraint” in evolution is clearer or more helpful than avoiding the term entirely in favor of more precise language (Olson 2012, 2019; Olson et al. 2019).

And yet thinking about “constraint” has inspired one of the most important advances of the past 30 years in empirical research regarding the causes of organismal trait distributions. This advance is, when confronted with a pattern of trait covariation such as the leaf lifespan–leaf mass per unit area scaling relationship, to ask whether the morphologies corresponding to the empty spaces that surround the scaling line can be produced developmentally by plants, and if so, whether they are of higher or lower fitness than the commonly observed

morphologies (Conner et al. 2011; Donovan et al. 2011; Olson 2012; Olson and Arroyo-Santos 2015). Finding that the “empty space” morphologies can be produced, but that they are of lower fitness than the common morphologies, is consistent with the hypothesis that the scaling relationship is one maintained by selection. Finding that the “empty space” morphologies apparently can’t be produced by plants, and that if they could, they would likely be of even higher fitness than the common morphologies along the scaling line suggests that some feature of development (that would require elucidation) impedes access to those areas. Note that while the term inspired these approaches, such thinking does not require use of the term “constraint” in any way, illustrating one way that rigorous overcoming of vague terminology can lead to major theoretical and empirical advances (Olson 2019).

### Stress

Ecologists spend a great deal of time studying “stress” of various sorts including drought, cold, and heat stresses. The notion of “stress” makes most sense in an agricultural setting, where a given plant variety is known to be able to produce some maximal yield under a certain set of conditions. A farmer can legitimately think of conditions that lower yield from this maximum as “stress.” However, in a natural situation, there is no meaningful maximal yield, performance, or fitness value but instead simply the conditions that an organism is exposed to and its reactions to it (Körner 2012, 2018; Anfodillo et al. 2016). The metaphor of “stress” can easily be dispensed with, by thinking in terms of natural selection. Organisms are subject to certain conditions, which can vary over time or between microsites. Under certain conditions, some individuals will have higher performance or fitness than others. There is no need at all for the term “stress” under this formulation, and indeed the term adds no useful insight. For example, an ecologist might wish to study the effects of drought stress on plant hydraulic evolution, subjecting experimental plants to well-watered and drought stress conditions, and finding that the “stress” conditions are associated with a certain degree of mortality. The “stress” metaphor in this and all other cases is entirely dispensable, as follows. Populations are made up of individuals that vary heritably in their characteristics. The conditions of natural selection vary over time or space. Different conditions are associated with differential fitness in different heritable variants. This formulation is all that is required to

dispense entirely with notions of “stress.” Other options include translating replacing “stress” with rigorous quantitative expressions. For example, most of the individuals of a species will fall close to scaling slopes between many traits, e.g., total leaf area and stem diameter. Herbivores removing leaves or trunk are often regarded as “stresses.” But the metaphor can be entirely dispensed with by the prediction that distance from the scaling line imposed by alteration of leaf–stem proportionality by herbivores (or pruning or other damage) should be associated with a reduction in performance, with larger displacements being associated with greater recovery times and greater performance reductions (Anfodillo et al. 2016).

Given that the term “stress” adds nothing to the description of nature, it often seems that the term does more harm than good, e.g., quantification of “stressful habitats,” or even quantification of “habitat harshness” (Marks et al. 2016), which represent circular reasoning. Habitats are identified as “harsh” or “stressful” because of low maximum plant stature, and low stature is explained by appeal to the harshness of the habitat. These problems of circularity are avoided by simply regarding the effects of differing selective contexts on the range of variation present or producible within populations, illustrating the ways that replacing vague terminology leads to a vast increase in precision.

### Plant evolutionary ecology pioneering examples for an expanding evolutionary biology

As indicated above, whether it constitutes an “extended synthesis” or not, current evolutionary thinking includes a richness of entities, processes, and conceptual sophistication absent from conventional MS thinking. Many of these ideas are currently of great interest, and plant evolutionary ecology has vast potential to contribute to these debates in multiple ways. Here I summarize three, one in which plant evolutionary ecologists have been foundational in building theory and data, and two others in which the potential for contribution is especially promising.

#### Niche construction

The MS largely viewed diversity in organismal lifestyles as being the result of diversity in environmental selection pressures. Occupied adaptive zones denote ways of life that are favored by selection, and empty spaces in adaptive zone space denote conditions that natural selection does not favor (Simpson 1953). An extreme version of this view

was vigorously criticized as viewing organismal niches as real and existing independently of organisms, with the world thus made up of “problems” for organisms to “solve” (Lewontin 2000). Yet biologists, and especially plant ecologists, have long known that organisms affect the conditions of natural selection that they themselves are subjected to. Motile organisms choose the parts of the landscape they inhabit and therefore the conditions they are subject to. All organisms, sessile or motile, alter their surroundings in ways that benefit them, conspicuously in animals such as moles, whose tiny eyes, paddle like hands, and collapse-resistant spine are clearly the products of selection in the context of life in burrows that the mole itself makes. Some authors regard the inseparability of organism and environment as requiring a novel set of theoretical and empirical tools, designating them with the term “niche construction,” with information from plant ecology providing essential concepts for the founding of niche construction theory (Odling-Smee et al. 2003; Archetti 2015). Others argue that thinking about the ways that organisms affect their own conditions of selection has been present in biology long before the niche construction term was coined (Brodie 2005; Futuyma 2017). However it is regarded, plant evolutionary ecologists have without a doubt helped to pioneer the niche construction perspective.

Plants are consummate niche engineers, drastically altering their surroundings, and the selective environment acting on themselves and their offspring. It is not only people who appreciate the cool shade of deep forest, with its soft cushion of leaf litter, but trees themselves also experience their own effects on microclimate and soil quality. In a recent paper, Bigelow and Canham (2015) found that the litterfall behavior of species in mixed deciduous forests in North America led to soil attributes that were favorable for the resource use patterns of each species. Schweitzer et al. (2018) review the evidence and theory regarding the potential for such interactions to be subject to selection, finding both strong theoretical reasons and empirical evidence consistent with soil conditioning niche construction to vary heritably between individuals within populations, and that this variation can have profound fitness impacts. Many of these effects are transgenerational, even potentially constituting “parental care by trees” in which the soil conditioned by the mother favors offspring. These and many other aspects have made plant evolutionary ecologists pioneers of the study of niche construction, and have shown that the reciprocal influences between organism and environment are important biological phenomena meriting study in

their own right, a message of relevance to all of evolutionary biology.

Many more opportunities for contributions remain. For example, some plants that require fire for reproduction would seem to be self-evident examples of niche construction. Eucalypts that carpet forests and woodlands with abundant, oil-rich bark, and leaf litter that burns readily, thereby excluding many non-eucalypts and allowing germination of conspecifics, would seem like a textbook example. Yet some authors sound a cautionary note. They reference the broader debate regarding the dangers of drawing conclusions regarding the adaptive status of a trait from its current function (Griffiths 1992; Olson and Arroyo-Santos 2015). The simple fact of a trait having an apparently useful role does not necessarily indicate that the trait was favored because of that role in the current or any other selective context (Gould and Vrba 1982; Garson 2016). A ready example is the human heartbeat, which is very useful in diagnosing heart conditions but heart presence clearly was not selected because of that role. By the same token, just because eucalypt litter is flammable might not mean that this flammability was favored by selection because it promotes the persistence of eucalypts (Bowman et al. 2014). Flammability and other examples illustrate that plant evolutionary ecologists increasingly turn to questions regarding the function of organismal traits. “Function” only makes sense in a biological context as the product of natural selection, as the heartbeat example illustrates (Garson 2016). Over the past 40 years, as part of the so-called “debate over adaptationism” (Griffiths 1992), evolutionary biologists have forcefully reworked the essential concepts necessary for studying the causes of organismal trait distribution. These causes include adaptation. Plant evolutionary ecology urgently needs to connect with these conceptual advances (summarized in Olson and Arroyo-Santos 2015) in its efforts to study the causes of trait variation, from vast patterns of trait covariation, to notions of trait “function” in physiological studies. As for adaptations generally, identifying whether a given trait was indeed favored in the context of the current niche construction environment remains a major frontier of opportunity (Olson and Arroyo-Santos 2015; Schweitzer et al. 2018). Another outstanding question would seem to be why very coarse scale environmental data, such as WorldClim climate layers (Hijmans et al. 2005), can so often predict organismal trait values with such precision (e.g., we found that precipitation variables from WorldClim predicted the wood mechanical stiffness across a clade of tropical trees with an  $R$  of 0.96) (Rosell et al. 2012). To what

degree such plant–climate relationships actually involve niche construction, or whether they are examples of a situation in which niche construction is unimportant, remains to be addressed.

### Developmental systems theory

A compelling facet of post-MS evolutionary biology is Developmental Systems Theory (DST), and because DST has not yet been taken up in all its aspects by empirical biologists, much territory remains to be explored, with plant evolutionary ecologists being some of the best-positioned to do so. “Development” in this context refers to ontogeny, the building of a new individual that resembles its parents. The novelty of DST is that it focuses on *developmental systems*, rather than genes, as the unit necessary to construct a new individual. A developmental system is the minimal set of participants—genes, lipids, proteins, water, temperature, light, etc.—necessary to build a new individual. DST is built on a series of tenets (Oyama et al. 2003). One of the main tenets of DST is *extended inheritance*, the empirical reality that DNA is a necessary element in development but by itself insufficient to construct a new individual. Instead, many factors, genetic and extra-genetic, are required. Related tenets are those of *distributed causation* and *causal parity*. These emphasize that there are no privileged agents or causes in ontogeny. Distributed causation refers to the fact that DNA does not direct ontogeny any more than a queen ant directs the nest (Gordon 2010). Instead, just as ant colony foraging behavior emerges as the result of the simple decision algorithms of each individual ant, ontogeny is a process of interaction among parts, no one of which can be identified as causally central. Causal parity reflects the empirical reality that in ontogeny DNA is just as important as lipids, water, oxygen, photons (see the remarkable example of the role of photons in eye development in Rao et al. 2013), or other crucial participants. Another central tenet is *development as construction*, the observation that there is no representation of the adult immanent within the genome. DST remains largely a theoretical effort, with practically no empirical biologists claiming to work on DST.

Plant evolutionary ecologists seem ideally poised to transform DST into an empirical research program. Plant species succession in a community of species is a prime example, providing a rich source of empirical information relating to all of the main DST tenets. Some species preferentially establish in clearings and others requiring the moist shade of established forest. The climax species that requires still, moist shade

receives these conditions necessary for its development from previous generations, illustrating extended inheritance and causal parity because not only genes are required for the establishment of a new climax species individual; the species will not establish without the needed moisture, shade, and humidity. Many more examples could be offered, but this is sufficient to suggest that the vast body of ecological thinking on succession offer a rich source of empirical data that could be drawn on by students of DST. By the same token, plant evolutionary ecology seems to stand to gain from an exchange with DST. For example, it is clear that DNA is necessary but not sufficient for constructing a new individual. This means that the set of components necessary for development goes beyond the DNA. This also implies that what is inherited between generations is not just genes, but the entire set of components necessary to reconstruct ancestral phenotypes, the so-called “developmental system” that gives DST its name. This notion leads to a radical reconceptualization of the definition of evolution from the MS notion of change in allele frequencies to change in the developmental system. This means that identifying the set of components necessary for reconstructing ancestral phenotypes, making up what is often referred to as the developmental niche (Stoltz 2017), should be a central priority for biologists. Yet virtually no studies attempt to characterize the developmental niche. It is not even clear how to do so, and what the “minimal set of developmental components” should be considered to include. These enormous outstanding issues mean that taking DST seriously provides very important direction for empirical research, with plant evolutionary ecologists being ideally placed to take advantage of this direction.

### Genes-as-followers evolution

A major criticism of MS theory involves the sheer implausibility of adaptation acting on variation generated solely by mutation. The criticism goes that a population subject to a given selection pressure has to wait around for just the right mutation, which when it eventually appears will do so in just a single individual. This individual then has to survive all of the random factors that beset a lone juvenile—getting hit by a beaver-felled tree, or, if the organism is a tree, being felled by a beaver. Somehow that good mutation, present in that lone and vulnerable individual, must, via its ever so slight effect on fitness, proliferate through the population. West-Eberhard (2003) refers to the “naked ignorance” of the persistent credence given to such a scenario.

From this point of view, “genes-as-followers” evolution (Schwander and Leimar 2011) is vastly more probable (Pigliucci and Murren 2003). This scenario involves the following sequence. First, a population is subject to a change of environment, either because of some change in selective environment *in situ* or migration. This change will be associated with phenotypically plastic responses, not in just a single vulnerable individual but in virtually all the individuals. Moreover, these plastic responses increase plant performance in the novel environment when compared with the performance that the phenotype produced in the ancestral environment would have in the current one. Via these phenotypically plastic responses, virtually all of the population has made important phenotypic steps in response to the novel environment, while the individuals in the population evolving via the traditional mutation-driven model would all bear a less-fit phenotype, still waiting for a mutation to arise. Once the population has responded via phenotypic plasticity, a variety of mechanisms, mostly invoking selection acting on standing variation in the ontogenetic thresholds that produce plastic responses, can stabilize these novel phenotypes (Pigliucci and Murren 2003; West-Eberhard 2003; Moczek 2007; Schwander and Leimar 2011). Down the road, the slower processes of mutation-driven selection can, to be sure, contribute to further these adaptive changes under novel selective conditions. These should occur much later than the rapid stabilizing of plastic responses, so that is why this view is referred to as “genes-as-followers” evolution. For the same reason that the genetic–plastic distinction is invalid, this form of adaptive evolution is probably better thought of as “development-” or “plasticity-” first evolution (Moczek 2007; Levis and Pfennig 2016), but “genes-as-followers” marks a useful contrast with the traditional view.

While plasticity-first evolution appears plausible, empirical case studies are still few, and because plant ecologists have a rich legacy of studying adaptation and plasticity, not to mention that plants are often tractable study systems, plant evolutionary ecology seems ideally poised for shedding light on this issue. One way of gathering direct evidence regarding plasticity-first evolution is to compare ancestors and descendants, which are abundantly available in domesticated plants and their wild ancestors, or between ancient seeds and contemporary populations. Exposing the ancestors to the derived environment should lead to the plastic production of a phenotype in the derived direction, among other predictions consistent with plasticity-first evolution (Ehrenreich and Pfennig 2016; Levis and Pfennig 2016).

Abundant robust evidence in favor of plasticity-first evolution would be revolutionary. It would imply that adaptation can be much faster and much more directed than traditionally supposed by the MS (Pigliucci and Murren 2003). It would imply, also, that modeling of adaptive processes would require substantial reconceptualization, and would add yet another reason to reject the genetic–plastic distinction. As a result, gathering empirical evidence for plasticity-first evolution has potential for vast interest and impact on plant evolutionary ecology and evolutionary biology at large. Despite this promise, and useful guides for what to look for in empirical studies (Ehrenreich and Pfennig 2016; Levis and Pfennig 2016), case studies remain scarce. In such paradigmatically plastic organisms as plants, understanding how the ranges of within-species plasticity facilitates interspecific functional diversification is surely a promising horizon.

## Conclusion

With its increasing focus on understanding the causes of plant trait distributions, across clades as well as within (Edwards et al. 2014), and its rich history of study of factors such as niche construction, plant evolutionary ecology is increasingly impinging on evolutionary issues far beyond the strictures of the traditionally construed MS. This convergence on evolutionary questions from a starting point in ecology brings positive and negative aspects. On the negative side, ecologists re-invent debates long examined in evolutionary biology without always taking advantage of the progress made in evolutionary biology, as in the debate over adaptationism (Olson and Arroyo-Santos 2015; Garson 2016) or the frequent misconstrual of evolution as linear progress (Rigato and Minelli 2013; Olson 2014). On the positive side, though, is that plant evolutionary ecologists engage, and have engaged for as long as the field has existed, with an unparalleled richness of biological situations, from vast patterns of trait relationships spanning all plants (Wright et al. 2004) to fine-scale patterns of species succession, situations that offer deeply innovative perspectives not only for plant science but biology as a whole. So, while the giant may still be dozing on some issues, and might need to check a map here and there, it is clearly out of bed and confidently striding in the right direction.

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