

## OPINION

# Darwin in the garden: Engaging the public about evolution with museum collections of living objects

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## Societal Impact Statement

Polls continue to show distressingly high percentages of people around the world do not accept that evolution has occurred. Even among individuals who accept evolution, surveys indicate that many do not understand its mechanistic basis, natural selection. Botanical gardens and arboreta are typically not viewed as museums of natural history. Yet, these institutions house collections of living museum objects that can allow visitors to directly observe ongoing evolution, namely, mutations and the origin of biological novelty, the astonishing amount of variation within species, and the consequences of selection that underlie descent with modification. When botanical gardens and arboreta are reconceptualized as museums of *living, evolving objects*, there will be huge opportunities to engage and educate the public about the process of evolution through the lens of horticulture and botany.

## Summary

Plants are central to the evolutionary history of biodiversity on Earth. However, unlike most museums of natural history, botanical gardens and arboreta are typically less engaged in the important mission of promoting the public's understanding of evolution. As museum collections of living (and evolving) objects, botanical gardens and arboreta have a unique set of opportunities to teach the public about evolutionary processes in ways that complement the efforts of traditional natural history museums. Charles Darwin himself relied heavily on his extensive reading of the horticultural and botanical literature to gain insights into evolutionary process and, after publication of *On the Origin of Species*, made plants the frequent centerpiece of his many books to convince the world of natural selection and descent with modification. There is good reason to believe that Darwin's highly effective 19th century botanical tactics for promoting evolutionary ideas among scientists and the broader society remain equally compelling today in the 21st century.

## KEYWORDS

Arboretum, botanical garden, Darwin, evolution, museum, public education

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## 1 | INTRODUCTION

Perhaps no one in history has made a more compelling case for the use of horticultural and botanical knowledge to promote an understanding of evolution than Charles Darwin. Darwin wisely and opportunistically looked to the worlds of horticulture, plant domestication history, and botanical gardens to gain critical insights into the roles of mutation, variation, and selection that underlie descent with modification. In turn, he used this knowledge to advance and relate evolutionary concepts to fellow scientists and the public in powerful ways.

Over the course of his lifetime, Darwin published 55 notes and articles in the *Gardeners' Chronicle and Agricultural Gazette* (Friedman, 2013), as well as 15 notes and articles in the *Journal of Horticulture and Cottage Gardener*. Horticulturally based insights are prominent in *On the Origin of Species* (Darwin, 1859), as well as the two-volume treatise *Plants and Animals Under Domestication* (Darwin, 1868). Throughout the “post-Origin” portion of his life (1860–1882; although note that Darwin ultimately produced six editions of *Origin*, the last in 1872), Darwin returned often to botanical topics in book form to make his case for the process of natural selection and evolution (Figure 1). From the pollination biology of orchids to the behavior of climbing plants, Darwin enlisted plants to advance a broader understanding of natural selection as a means to adaptation and evolutionary change.

Tellingly, Charles Darwin devoted the entire first chapter of *On the Origin of Species* to “Variation under Domestication”. Darwin did not look first to nature to build a case for variation and the process of selection, but rather to the domesticated worlds of fancy pigeons, dogs, cattle, rabbits, sheep, dahlias, heartsease, apples, pears,

gooseberries, and strawberries. As Darwin so clearly understood, documenting the origin of biological novelty, the extent of variation, and the role of human selection in domestication history, provides a powerful context for extrapolation from the effects of variation and selection over the course of a human lifetime to the effects of variation and selection over the course of geological ages. Darwin puts the case concisely in the concluding chapter of *Origin* (Darwin, 1859): “There is no obvious reason why the principles which have acted so efficiently under domestication should not have acted under nature. In the preservation of favoured individuals and races, during the constantly recurrent Struggle for Existence, we see the most powerful and ever-acting means of selection”. We ignore, at our own peril, the power of Darwin's strategy of introducing the world to evolutionary thinking if we overlook the extraordinary value of horticultural and botanical collections and the import of domestication history.

## 2 | BOTANICAL GARDENS ARE NATURAL HISTORY MUSEUMS WITH UNIQUE OPPORTUNITIES TO TEACH EVOLUTIONARY CONCEPTS

Museums of natural history have done much to promote a robust public understanding of the evolution of life over the last 3.5 billion years (Diamond & Kocielek, 2012). Any visit to a museum of natural history would be difficult to complete without encountering dinosaur and other fossil evidence of the past diversity of life on Earth. Moreover, modern natural history museums have developed and promoted experiential and interactive presentations of content related to evolutionary theory, pattern, and process. Considerable exhibition space is now routinely dedicated to the explanation of the roles of mutation, variation, and natural selection in generating biological novelty and evolutionary change over time (Diamond & Kocielek, 2012; Spiegel et al., 2012). Nevertheless, surveys of natural history museum visitors indicate that while a majority adhere to broad aspects of macroevolutionary pattern and history, far fewer understand the mechanism of natural selection as a driving force for evolutionary change (Evans et al., 2010; MacFadden et al., 2007). These findings echo studies of American students that show that even among those who hold an evolutionary view of biodiversity, a substantial portion still struggle to correctly understand the process of natural selection (Evans et al., 2010). Even more troubling, a distressingly large percentage of Americans believe either in the miraculous creation of biological species or subscribe to a “designed” or guided evolutionary process (Brenan, 2019; Miller, Scott, & Okamoto, 2006; Pew Research Center, 2013, 2019). Europe and other parts of the world also suffer from a persistent and growing anti-evolutionist set of movements (Blancke, Hjermslev, & Kjaergaard, 2014).

In the pedagogical literature focused on educating the public about evolution in the classroom and in natural history collections, botanical gardens are never discussed (e.g., Diamond & Kocielek, 2012; Evans et al., 2010; MacFadden et al., 2007; Spiegel et al., 2012). In the literature focused on studying and teaching



**FIGURE 1** First editions of Darwin's post-Origin books on plants. *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects* (1862); *The Variation of Animals and Plants under Domestication* (1868); *The Movements and Habits of Climbing Plants* (1875); *Climbing Plants* was originally published in the *Journal of the Linnean Society of London, Botany*, in 1865; *Insectivorous Plants* (1875); *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom* (1876); *The Different Forms of Flowers on Plants of the Same Species* (1877) and; *The Power of Movement in Plants* (1880)

evolutionary processes and concepts, “natural history museums” or “natural history collections” do not include botanical gardens and arboreta (see for example Diamond & Evans, 2016; Holmes et al., 2016), although herbaria may be included under this overarching view of what constitutes a collection of natural history objects. This is regrettable, although responsibility for this absence also lies with botanical gardens and arboreta themselves since there is often less emphasis on visitor education around the topic of evolution. Rather, important global challenges such as climate change, conservation, restoration ecology, sustainability, invasive species, and ecosystem services are the frequent foci of scientific outreach efforts by botanical gardens (Blackmore, Gibby, & Rae, 2011; Powledge, 2011). Yet, these biological collections of *living objects* are also ideally suited to educate the public about evolutionary processes in powerful ways. This is where the important distinction between evolutionary *pattern* and evolutionary *process* is crucial—and the difference between *dead* and *living* museum objects is important to note and understand.

Museums of natural history almost exclusively house non-living objects. In the biological realm, these comprise fossils or the preserved remains of recently living organisms. These museum objects are invoked to teach about biological diversity, adaptation, evolutionary history, phylogenetic relationships, and increasingly, variation and the process of natural selection. Such evolutionary evidence speaks effectively to macroevolutionary pattern, but often less so (or less effectively) to microevolutionary process—precisely what visitor surveys indicate the public has difficulty understanding (Evans et al., 2010; MacFadden et al., 2007). Botanical gardens, as collections of living objects, can allow visitors to directly observe the very stuff of ongoing evolution, namely, mutations and the origin of biological novelty, the extent of variation to be found in nature, and the consequences of selection that underlie descent with modification. Moreover, botanical gardens and arboreta have a unique opportunity to introduce the public to evolutionary thinking in ways that are less “threatening” (i.e., do not involve *Homo sapiens*) to individuals uncomfortable with discussions of human origins. When botanical gardens self-identify as and are viewed as museums of natural history, much can be accomplished to help the public gain a better understanding of the magnificent process of evolution that has created extant biodiversity.

### 3 | OBSERVING EVOLUTION: THE POWER OF LIVING MUSEUM OBJECTS

A challenge often aired by the “skeptical public” (now and in Darwin’s day) is that evolution cannot be seen; thus, how can we be confident that it occurred and is occurring? Connecting macroevolutionary *patterns* of the diversity of life in natural history collections to the actual generation of variation and *process* of natural selection has proven difficult. Botanical gardens and arboreta present a unique set of opportunities to powerfully demonstrate that evolution is happening all around us and can indeed be seen and witnessed; living museum objects are ideally suited to this role.

Collections of living plants can showcase how the process of natural selection works in three distinct ways. First, collections of horticultural variants (often single-gene mutant phenotypes) can help the public understand how evolutionary novelties arise and that such mutations are not uncommon. Second, phenotypic variation among individuals of a species in botanical gardens and arboreta can vividly display the sheer abundance of raw materials that allows the process of selection to favour and disfavour variants. Botanical gardens represent a human obsession with finding rare and aesthetically pleasing deviants (from “type”) in nature. Finally, documentation of the short-term process of human domestication (artificial selection) can illustrate the long-term process of natural selection and evolutionary change. If teosinte can be transformed into modern maize in a mere 9,000 years (Yang et al., 2019), the public can be encouraged to extrapolate to what can happen over the course of millions and billions of years.

### 4 | HIGHLIGHTING MUTATIONS AND THE GENERATION OF BIOLOGICAL NOVELTY USING LIVING MUSEUM OBJECTS

Novel plant phenotypes are regularly discovered in natural populations, in botanical gardens, and in horticultural nursery operations. These variant phenotypes, when formed from mutations in a shoot apical meristem, are referred to as “sports”, or what Darwin called “bud-variations”. Because all plants are continuously embryonic and produce new organs (leaves, stems, reproductive organs) from apical meristems throughout their lives, mutations can be easily detected and propagated. Sports reveal themselves when a branch or set of branches differ significantly from the original phenotype of the rest of a plant.

As a consequence of the human desire for rarity and novelty, mutant forms of plants are coveted and propagated, and botanical gardens and arboreta are filled with clonally propagated sports. Indeed, there is no other kind of natural history collection or place in nature where such large numbers of obviously mutant organisms are gathered in one location. As such, these horticultural cultivars are the ultimate object-based educational tools to demonstrate that spontaneous genetic mutations, the essential raw materials for variation, occur regularly. The display of such mutant phenotypes side by side with conspecific plants exhibiting the original wild type phenotype presents a clear opportunity to educate the public about the origin of biological novelty in the evolutionary process. Additionally, such cultivars can be used to explain genetic mechanisms associated with the evolutionary origin of novel morphology, architecture, and patterns of pigmentation. Behind every horticultural sport is a potential narrative on the origin of a genetically-based novel phenotype and its ability to potentially spread within a population. This is truly “evolution in action”, with evolved and evolving *living museum objects* on display.

Floral mutants have long captivated horticulturists and natural historians, and indeed, Charles Darwin himself was curious

throughout his life about the developmental origins of such flowers (Darwin, 1843, 1868). Many double flowered horticultural sports involve a dramatic homeotic transformation of floral organ types and have been extensively studied by developmental biologists (Kramer, 2007; Meyerowitz, Smyth, & Bowman, 1989; Theißen, 2010). Sports displaying changes in floral symmetry can also vividly demonstrate the role of mutation in the evolutionary process. A commonly documented shift in floral symmetry involves a transition from the production of bilaterally symmetrical flowers to radially symmetrical (peloric) flowers (Figure 2). Peloric mutants have been discovered (in nature) in a broad range of angiosperm families (Cubas, Vincent, & Coen, 1999; Hasing et al., 2019; Jabbour, Nadot, Espinosa, & Damerval, 2016; Rudall & Bateman, 2003)—all of which can be easily grown and displayed in gardens. Darwin himself (Darwin, 1868) performed crossing experiments and studied the inheritance of pelorism in snapdragon, *Antirrhinum majus*. Educational materials on peloria in foxgloves (*Digitalis purpurea*) have been wonderfully developed at Royal Botanic Gardens, Kew, with web-based discussion of the potential evolutionary significance of such heritable morphological changes (Rudall, 2016). Importantly, changes in floral symmetry, as well as floral coloration and patterning, often result from simple genetic changes and are well known to be associated with major shifts in pollination biology (Hopkins & Rausher, 2014; Moyroud & Glover, 2017; O'Meara et al., 2016; Sheehan et al., 2016; Yuan, 2018). As such, these sports can be used to link biological novelty to adaptation.

Many horticultural sports are associated with plant architecture and/or vegetative morphology (Darwin, 1868). Weeping forms of trees have arisen innumerable times and typically the origin of such pronounced variants is well documented in natural populations (Del Tredici, 1980; Gallois, Audra, & Burrus, 1998; Figure 3). Cutleaf cultivars of herbaceous and woody plants are common in the horticultural trade and gardens. These sports show pronounced alterations from the wild type of leaf morphology (Figure 4), with deep sinuses that suggest fernlike foliage. Importantly, these mutants mirror the evolved diversity of leaf forms found among species in a wide diversity of clades of flowering plants. Unlike many floral mutants, these vegetative mutants are not yet well characterized at the level of genes and developmental biology.

Botanical sports are not only found in nature but have arisen on the grounds of botanical gardens and arboreta. For purposes of

outreach and education, nothing can surpass a visible mutation that evolves in situ. Such events are the ultimate object-based demonstration that spontaneous genetic mutations, the essential raw material for variation, occur regularly. A striking instance of a mutation event occurred in a redbud tree, *Cercis canadensis*, at the Arnold Arboretum (Friedman, 2013). A set of branches bearing nearly white flowers could easily be seen against the wild type pink flowers on the remainder of the tree (Figure 5). This bud sport mutation has been used for public education programming as a vivid reminder that evolution can be “witnessed” and that it is happening all around us.

## 5 | NATURE'S VARIATION IN A GARDEN BED

Beyond individual sports, botanical gardens and arboreta have the opportunity to broadly demonstrate the magnitude of variation present in nature. Horticultural practice seeks out botanical variants and puts such genetic variation to work. A simple bed of heartsease, *Viola tricolor*, with every possible floral color or patterning demonstrates the magnitude of genetic variation on offer to selection (in the wild, and for domestication purposes) at any one moment in time. Indeed, in *Variation*, Darwin (1868) devoted nearly two full pages of discussion to variation of *V. tricolor* “in the size, outline, and colour of the flowers”, leaf shape, and even the diverse forms of the nectary. Botanical garden beds, particularly of annuals or herbaceous perennials, provide excellent opportunities to explain that what is on show are vast amounts of genetic variation, the raw materials for selection.

## 6 | DOMESTICATION HISTORY—DEMONSTRATING THE POWER OF SELECTION

In *Origin*, Darwin highlighted the domestication history of plants (and animals) in order to advance his arguments about the process (selection) and pace (slow, steady, ultimately impressive) of descent with modification over hundreds or thousands of years. In essence, Darwin asks the reader to extrapolate the pronounced effects of



**FIGURE 2** Left, wild type zygomorphic (bilaterally symmetrical) flower of florist's gloxinia, *Sinningia speciosa* (cultivar 'Darth Vader'). Right, mutant actinomorphic (radially symmetrical) peloric flowers of florist's gloxinia (cultivar 'Buzios'). Photographs courtesy (and with permission) of Tomas Hasing and Aureliano Bombarely





**FIGURE 3** The magnificent 'tortuosa' European beech, *Fagus sylvatica* f. *tortuosa*, displays a remarkable form of twisted branching and can be found in wild populations in France, Germany and Sweden (Gallois et al., 1998)

domestication history to evolutionary time scales (Darwin, 1859): "Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some

way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations"?

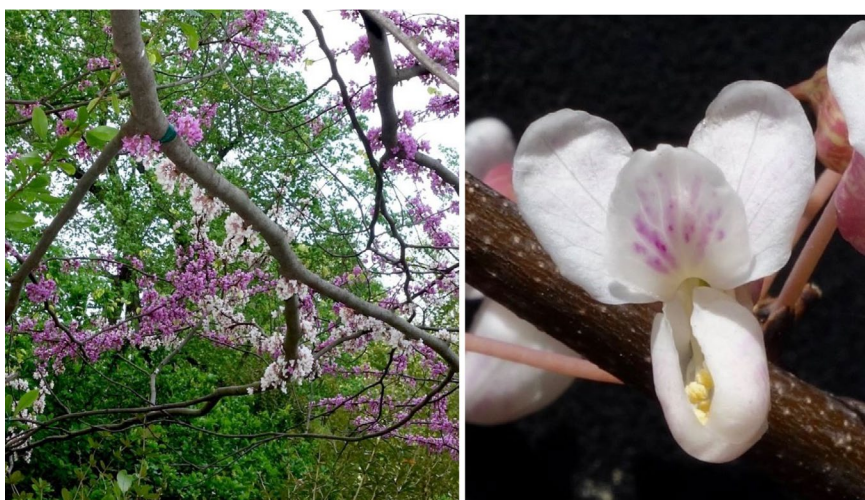
Botanical gardens have highlighted the roughly 10,000 years (Doebly, 2006) of plant domestication history. However, these displays are not typically invoked to link artificial selection and domestication history to the process of natural selection over the course of evolutionary history as Darwin did. Displays of ancestral wild species and their domesticated descendants in botanical gardens, when explicitly used to demonstrate the cumulative power of selection (as well as the role of mutations), present a key opportunity to educate the public about the means, pace, and potential for descent with modification when scaling from mere thousands of years of domestication history to millions and billions of years of Earth's history.

Darwin might well be astonished to learn what we now know of the domestication history of any of a host of crop species whose genomes (Miller & Gross, 2011) have been interrogated. In the cases of pears and apples, both featured in the first chapter of *Origin*, modern genomic analyses reveal genes of importance

**FIGURE 4** *Quercus dentata* 'pinnatifida' (right), the daimyo oak of eastern Asia is a cutleaf mutant form of the wild type leaf (left)



**FIGURE 5** A bud sport of *Cercis canadensis* (eastern redbud). Left, the mutant light-colored flowers are present on a single system of shoots on a parent wild type plant. Such bud sports are commonly discovered and propagated (cloned) for introduction into the horticultural trade and botanical gardens and arboreta. Right, the mutant flower lacking a pink background on all of the petals, but retaining the nectar guides on the upper banner petal



during domestication, the identity of wild progenitors, as well as the admixture of wild species as domesticated varieties moved along trade routes (Cornille, Giraud, Smulders, Roldán-Ruiz, & Gladioux, 2014; Wu et al., 2018). A domesticated pear or apple placed next to an undomesticated member of the ancestral species (and perhaps tasted in a public program), along with those species that have been involved in introgression, can be invoked to explain the kinds of transformations in characters that have occurred over thousands of years of domestication history. The European wild cabbage, *Brassica oleracea*, and its domesticated descendent crops (cabbage, broccoli, cauliflower, Brussels sprouts, kohlrabi) provide an astounding array of opportunities to discuss selection and divergence from a common ancestor over just a few thousand years (Maggioni, Bothmer, Poulsen, & Lipman, 2017). Examples of botanical gardens featuring domestication history of crops abound. Royal Botanic Garden Edinburgh has created public programming comparing the flavors of domesticates versus wild ancestors for a number of crops, including wild cabbage (Coleman, 2015). Wuhan Botanic Garden displays a diverse collection of *Actinidia* (kiwi) cultivars and wild species in close proximity (Krishnan et al., 2019). The key to extending the reach of such displays of domestication history is a direct linkage to the process of natural selection and longer-term character transformations over the course of evolutionary history.

Maize, of course, offers remarkable opportunities to discuss how major changes in phenotype transformed wild teosinte (*Zea mays* subsp. *parviglumis*) into the mouth-watering sweet corn enjoyed on a summer's day. The combination of recent archeological (Kennett et al., 2017) and genomic (Yang et al., 2019) advances now illuminates the specific order of domestication events in maize, including increases in the number of rows (and size) of kernels, the loss of shattering, changes in shoot system architecture, and the transition away from kernels fully encased in a hard shell (Flint-Garcia, 2017). Sum it up over 10,000 years and extrapolate to the evolutionary diversification of grasses over the last 80 million years (Christin et al., 2014), or angiosperms over the last nearly 140 million years (Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández, 2015), or land plants over the last 470 plus million years (Morris et al., 2017). Darwin's comments in *Origin*, that breeders of the day could scarcely imagine their domesticates were descended from wild progenitors so very different, still rings true today.

## 7 | ADDITIONAL OPPORTUNITIES FOR PLANT COLLECTIONS TO TEACH ABOUT EVOLUTION: HYBRIDIZATION, BIOGEOGRAPHY, AND PHYLOGENY

Beyond making the case for the role of mutations, variation, and selection, there are many other opportunities for botanical gardens and arboreta to teach evolution. Given the prevalence of interspecific hybridization in the creation of new plant species (Abbott et al., 2013; Folk, Soltis, Soltis, & Guralnick, 2018), botanical collections

have the opportunity to educate the public with displays of parental species and their hybrid progeny. Indeed, long before Darwin, the early evolutionist William Herbert (reckoned "the third most experienced hybridiser" by Darwin in *Origin*) was led to an evolutionary world view from his extensive hybridization work with amaryllises and many other flowering plants.

Gardens and arboreta are also in an ideal position to showcase biogeographic patterns of plant distribution around the globe. Darwin used Asa Gray's insights into eastern Asia—eastern North America temperate plant species disjuncts to great effect as he began to piece together the roles of migration, historical climate change, and speciation in the 1850s (Boufford & Spongberg, 1983; Dupree, 1959; Yih, 2012). Biogeographic patterns of plant distribution remain powerful reminders of Earth's dynamic and nomadic biological history. Of course, phylogenetic relationships of plants (probably the most common evolutionary content on display in gardens), as now revealed through molecular and genomic analyses, can be illuminated in living collections too.

## 8 | WHY DID CHARLES DARWIN FOLLOW ON THE ORIGIN OF SPECIES WITH A BOOK ABOUT THE POLLINATION BIOLOGY OF ORCHIDS?

One might well ponder the question of why Charles Darwin followed his masterpiece *On the Origin of Species* with *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects* in 1862 (Darwin, 1862). Wonderfully, Darwin has left us with a written record of his reasoning and tactics. In early July of 1862, shortly after the publication of *Orchids*, Asa Gray wrote to Darwin about having just read through an address by George Bentham, president of the Linnean Society of London. Bentham, who initially was greatly agitated by *Origin*, came to embrace and support its conclusions, but it appears to have taken some time (Burkhardt, Smith, Secord, Pearn, & Darwin, 1997). Gray wrote (July 2 or 3, 1862): "I have just received and glanced at Bentham's address, and am amused to see how your beautiful *flank*-movement with the Orchid-book has nearly overcome his opposition to the *Origin*". To which, Darwin responded (July 23 or 24, 1862): "Of all the carpenters for knocking the right nail on the head, you are the very best: no one else has perceived that *my chief interest in my orchid book, has been that it was a 'flank movement' on the enemy*" [emphasis added]. Darwin knew that plants were a critical portal into understanding evolution. Indeed, plants were the centerpiece of his 20-plus year post-*Origin* strategy of convincing the world that evolution is true.

## 9 | CONCLUSION

While it is not my intention to be proscriptive, it is my contention that botanical gardens and arboreta should strive to become more actively engaged in promoting societal understanding of the



microevolutionary processes that ultimately generate macroevolutionary patterns of life. Such efforts will require botanical gardens and arboreta to more explicitly self-identify as natural history collections. Importantly, a programmatic set of aspirations for botanical gardens and arboreta to create content that educates the public about the ongoing processes and underlying mechanisms of evolution has the potential to be both complementary to and synergistic with the efforts of traditional zoocentric natural history museums. Thus, traditional natural history museums, botanical gardens, and arboreta should seek to partner in ways that mutually reinforce evolutionary concepts when it comes to educating the public. It is time for botanical gardens and arboreta around the world to commit to leveraging their living collections of museum objects to explain and demonstrate the roles of mutation, variation, and selection in the evolutionary process. In doing so, much could be accomplished to increase scientific literacy at a societal level. Darwin certainly thought that plants were central to bringing the general public to an understanding of the processes associated with evolutionary change. Who are we to question Darwin's wisdom?

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