Ornamental plant domestication by aesthetics-driven human cultural niche-construction

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Keywords (4-6 words)

Aesthetics; cultural evolution; extended evolutionary synthesis; gene-culture coevolution; ornamental plant domestication; socio-cultural niche construction; symbolic-material assets.

Highlights

Ornamental plants are unique as their domestication is not associated with the need for food security but rather for human aesthetic, visual and other sensory attractiveness.

The new extended evolutionary theory – proposing that inheritance and evolution is not by genes alone but is affected by the environment and human socio-cultural processes, and by gene-culture coevolution – makes it possible to elucidate plants' evolution and domestication.

Ornamental plant domestication and breeding is a specific aesthetics-driven dimension of human niche construction, that coevolved with socio-economic changes and new scientific technologies.

The new era of ornamental plants is dependent on the application of new technologies and symbolic-to-material asset shifts, with a foundation in a human sense of beauty and aesthetic values.

Abstract

Unlike plants that were domesticated to secure food, domestication and breeding of ornamental plants are driven by aesthetic values. Here we examine the major elements of the extended evolutionary synthesis theory that bridges the gap between the biology of ornamental plant domestication and the socio-cultural motivations behind it. We propose that it involves specific elements of cumulative cultural evolution, plant gene-human culture coevolution and niche construction. Moreover, ornamental plant domestication represents an aesthetics-driven dimension of human niche construction that coevolved with socio-economic changes and the adoption of new scientific technologies. Initially functioning as symbolic and aesthetic assets, ornamental plants became globally-marketed material commodities as a result of co-dependence of human cumulative cultural evolution and prestige-competition motivations.

Plant domestication and the Extended Evolutionary Synthesis

The evolutionary history of flowering plants extends across ca. 125 million years. During this time, an intricate and variable assortment of more than 400, 000 different plant species has developed. It is estimated that a total of 2500 plant species have undergone domestication worldwide [1], and only a small fraction of these (200-250 species) have

been domesticated as sources of food [2, 3]. A few plant species were domesticated for construction timber and fire wood, for the paper industry and for fibers and weaving; however, in fact there are more ornamental plant species cultivated today than all other agricultural and horticultural crops for food combined [4]. Ornamental plants were domesticated for their ornamental and "showy" characteristics, for gardening, indoor decoration and as cut flowers, including an increasing number of species that have been domesticated only recently. The history, processes, key events and proposed theories of domestication have been described and discussed at length for food plants [5 - 7]; however, little attention has been given to ornamental plants and the interaction with human socio-cultural elements and sense of aesthetics.

The Extended Evolutionary Synthesis

Research on early evolution and domestication events has seen major advances over the last 50 years, and it fits well with the new extended evolutionary synthesis (**EES**, see Glossary) [8 - 10]. Whereas the early 20th-century "modern synthesis" concept of evolution merged Darwin's theory of evolution and Mendelian heredity as the sole factors [11], EES basically proposes that "there is more to inheritance than genes" [9], i.e., organism evolution in general (including plant evolution and domestication) cannot be explained by genetic concepts only. Rather, organisms' evolution is directed also by physical development, by the environment that shapes organisms' traits, by human socio-cultural processes, and by extra-genetic inheritance [8, 10]. Although still contested by a few scholars [12], see also a review of the debates [13], EES allows for a better overall understanding of evolution by combining three important intertwined and well-described processes - cumulative cultural evolution, **CCE**, niche construction, **NC**, and gene-culture coevolution, **GCC** - that bridge the gap between genetic evolution, the environment and human culture. We review these evolutionary concepts and explore how the new interdisciplinary approaches can contribute to the study of plant evolution and domestication. CCE refers to cultural transmission of knowledge and social learning from one person and from one generation to another, both intentional and unintentional, that result in evolutionary change in knowledge [14, 15]; GCC indicates

and explains how human cultural factors modify and shape their own or other organisms' gene expression and genetic evolution [16, 17]; NC is the process whereby organisms, through their activities and choices, transform and modify their own and other organisms' environments and niches; importantly, it also refers to the case where one population changes some aspect of the environment of another population that has selective consequences for it [18, 19]. GCC was initially focused on the evolution of functional genes in human populations [16, 17], and it was extended later to include also domesticated animals' and plants' genes [5, 20] and animals in general [21]. Several recent studies indeed indicate that the study of plant evolution and domestication, as well as the origin of agriculture, can benefit from being situated within EES theory [5, 22 – 25]. Here we join these, and others, and highlight how CCE, GCC and human NC yield new insights into ornamental plant domestication, breeding and global distribution. For a more comprehensive discussion of EES, CCE, NC and GCC see Key Figure 1 and Box 1.

Food vs. aesthetics considerations of domestication

While the underlying reasons for domestication and breeding of food plants are human needs for food [7, 26], the reasons for ornamental plants domestication and breeding combines **aesthetic considerations** of what is beautiful and attractive (referring to color, scent, shape, symmetry and more) that are influenced by personal preferences in judgement and human socio-cultural, ceremonial and symbolic values. Aesthetics concerns a large range of disciplines, from art and philosophy to social science, cultural history and physical forms, and thus has different and complementary meanings depending on the field in which it is defined. Here we use the term 'aesthetics' with respect to ornamental plants, i.e., "The value of ornamental plants relies on their aesthetic appearance, including pleasing flower and/or leaf color, flower and/or leaf shape, fragrance, leaf texture and variegation, and overall plant form or architecture" (27). The signals that drive aesthetics and 'beauty' can include neurotransmitters (neuro-aesthetics, as discussed below), sociological, psychological, practical and additional categories (28). It is becoming increasingly recognized that values of beauty and aesthetics, in their various forms, are an aspect of human evolution and that

aesthetic aspects of landscape, for example, are important for human well-being [28]. Ideals of beauty and aesthetic values are both a cultural asset and an essential dimension of human life [29 - 31]. Aesthetic values affected and shaped the domestication, breeding and cultivation of most ornamental plant species since millennia, although a few species are cultivated in addition for their use in remedies, perfumes etc. The role of human aesthetic values with respect to flower cultivation has been discussed in several publications [32 - 34]. Although Kant defined the garden as a visual art and considered that smell plays no role in its aesthetic appreciation and that the appreciation of a garden is the appreciation of its form, it is obvious that that most human senses (e.g., sight/vision, smell, touch) are part of the overall aesthetic appreciation of a garden (35). Moreover, recent studies point to coevolution of biological features and general aesthetic values. For example, as far as activity in the brain is concerned, there is a faculty of beauty that can be activated by musical and visual sources, and probably by other sources as well, and a brain-based theory of beauty has been formulated [36]. It has also been suggested that the human aesthetic sense is based on general principles of perception, including a preference for symmetry that have been important during the evolution of biological signals [29, 37]. The significance of the symmetry visible in many Paleolithic hand axes, an artefact form used by early hominins in many parts of the world from c.1.76M to after 300,000 years ago, has been extensively discussed but there is general agreement that it was intentionally produced, whether for signaling purposes of various kinds or simply for its own sensory rewards (38).

Cultural history and categories of ornamental plants

As far as we are aware, the earliest archaeological evidence of flowers and other ornamental plants includes discoveries of flowers, seeds and other relics in burial sites, and for religious ceremonies [39, 40]. Archaeobotanical remains are abundant in ancient

burial sites as offerings to the dead [41], because flowers had a symbolic meaning [42]. It has been claimed that flowers were intentionally placed with a Neanderthal burial, probably dating to 60,000-70,000 years ago in the Shanidar cave in present-day Iraq, on the basis of pollen grains found in the associated sediment (43). However, this claim has been disputed and the matter remains open (44). In addition, the golden face of Tutankhamun was found garlanded with fresh flowers exquisitely preserved for 3,000 years [45]. Recently, a preserved Natufian floral grave lining, dated between 13,700- and 11,700-years BP, was reported [46], and the authors claim that it provides the earliest known direct evidence for grave decoration with plants and flowers. These and other findings, including ancient written evidence, clearly indicate the presence of flowers and plants in ancient graves and the association they may have with humans. However, they do not in themselves support domestication, as the flowers may have been collected from the wild. In his monumental study "The culture of flowers", Goody [42] distinguished between specific uses of ornamental plants and their aesthetic values: "the term 'culture' is employed as a signpost to an arena of human performance, very much part of the social life... I speak of 'utilitarian' and 'aesthetic' horticulture in a similar way…". The collection, domestication, cultivation, and breeding of ornamental plants are evident in Europe especially since the 17^{th}-18^{th} century, concomitantly with the era of travelling to new countries and collection of new botanical species that resulted in an increased number of new hybrids [25]. Ornamental plants are cultivated mostly for their aesthetic values, either as cut flowers and potted plants, or other horticultural traits [4]. In addition, a few of those plants are used also in the perfume industry (e.g., rose, lavender, jasmine), in medicine (e.g., rose hips as source of vitamin C, *Catharanthus* (rose periwinkle) and *Vinca* for chemotherapy, in culinary routines and as thorny rose fences for defense. Trees - selected for their shape, crown architecture and symbolic values such as cypress and stone pine already since the Greek-Roman culture – can be likely considered as ornamental plants.

In the following we examine the driving forces of ornamental plant domestication and breeding that brought about the formation of a unique aesthetic-driven socio-cultural component of the human niche within the framework of EES, CCE and plant gene-human culture coevolution (Key Figure 1 and Box 1, Figure 2).

Case studies

The examined cases include categories of ornamental plants that diverge with respect to specific underlying reasons of their domestication and breeding, in different world regions and societies, their evolutionary history, and specific technologies and breeding approaches.

Roses

Rose represents an outstanding example of a long domestication history combined with multiple evolutionary targets, including beauty and decoration, that are due to aesthetic drivers, as well as for their use in defense and cuisine that can be referred in terms of practical applications. It is assumed that wild roses were first domesticated and later cultivated in China and Mesopotamia 5,000-4,000 years BP [47] and it is likely that the first domesticated roses correspond to propagation of species collected from the wild, which further led to spontaneous interspecific hybrids [48]. Aesthetic and ornamentation factors were the primary reason for secondary domestication events and spread of rose species in Western and Central Europe during the 14th-15th century [49].

The domestication and cultivation, and later breeding of rose species is evident especially since the 17th-18th century [50]. Nowadays, there are about 35 000 cultivated rose genotypes and phenotypes [47]. Molecular marker-assisted selection and whole genome sequencing of the rose genome has enabled accurate tracing of the genetic origin, more efficient breeding by combining the growth vigor of European rose species and the recurrent blooming of old Chinese species [51], and reconstructing secondary metabolites that regulate scent and flower color [52]. Additionally, combined genetic and genomic approaches have resulted in identifying potential genetic regulators of key traits [53], provided strong molecular evidence for rose origin and domestication

history, and enabled new gene expression and genome editing [54], including over expression of several anthocyanins compounds that resulted in a genetically modified "Blue Rose" [55].

The cultural history of roses represents an outstanding combination of plant gene-technology-human culture co-evolution, which resulted in breeding many new variants, each with specific marketing characteristics – all driven primarily by aesthetic and other horticultural values. Today, rose cut flowers account for approximately 30% of the global flower market [48]. The unique position of roses, from antiquity to present, represents a tour de force of combining patterns of beauty, showiness, attraction, fragrance, defense, cuisine, decoration, molecular biology, and – last but not least – worldwide market demand. Furthermore, the large rose genotype resources allowed for breeding for resilience under different climatic conditions, and more.

Tulips

Tulip domestication, breeding and commercial cultivation represents a prestige-driven establishment of a specific socio-economic niche during the Dutch **tulipmania** era**.** The first records of tulip domestication (and later cultivation) are from Persia, in the 10th century [56]. The major spread of tulip bulbs to Europe was first to Leiden University in late 1593 [56, 57]. All early visually-favoured tulip cultivars most probably emerged from natural hybridization in small gardens in the Near East and later in Europe [56]. The new era of tulip breeding activities became evident during the "Golden Age" of the Netherlands, resulting in the tulipmania period 1615 – 1638 [58 – 60]. The main drive for tulip breeding was the creation of new highly attractive, unique and extravagant marketable phenotypes. The first large-scale significant creation of new tulip phenotypes was due, at least in part, to an outbreak of a tulip disease caused by the Tulip Breaking Virus (TBV) that caused the formation of unique flower colors and variegations in tulip petals, hence "color breaking", and was first noted in the Netherlands around the beginning of the 17th century [61, 62].

This unprecedented breeding and cultivation of new tulip species and cultivars is one of the best examples of combined social- and economical-driven domestication and breeding of ornamental plants. It was most likely the financial strength and the unique position of the rich merchants of the Dutch United East India Company that led to the rush for exotic tulips, and they soon controlled tulip bulb breeding and marketing, aiming at upgrading their social status through financing the tulip breeding industry. As a result, they achieved both great profits and an elite status as collectors of unique tulips that became a badge of social status [59]. It is a unique example of the way in which ornamental plants that were first a status **symbol** soon became marketable **material goods** [63, 64]. The tulipmania era eventually resulted in the development of excellent breeding skills, and tulips soon spread to several other European countries thus creating a new socially-driven human niche dimension.

Bonsai

Bonsai domestication history is varied in the different woody plant species used for creating the bonsai practice, however here we refer only to the "taming" and cultivation (i.e., forming a bonsai plant) that follows earlier domestication. Bonsai is the practice and art of growing small plants, usually miniaturized trees, in containers, suggestive of a natural scene [65]. The practice of bonsai is perhaps the ultimate representation of how specific cultural-aesthetic values and principles, in this case traditional Japanese, were harnessed to create unique horticultural shapes and forms of living plants [66 – 68]. The Japanese philosophy that natural beauty becomes true beauty only when modified by humans was first mentioned at about 970 AD [69] and is a representation of the importance of combined knowledge of plant biology and physiology with cultural-driven aesthetic values and principles of forms and shapes. The practical principles of how to harness and control plant growth, with the purpose of dwarfing and creating specific bonsai shapes, required either a learned knowledge of all basic aspects of plant physiology and development, or acquiring it by trial and error, or both. It is difficult to assume that the 20th century scientific knowledge of plant developmental physiology was available to early Japanese horticulturists during the 7th- 8th century

AD. Accordingly, bonsai was most plausibly practiced first by a few people who observed the natural life of plants and modified growth by trial and error techniques, that improved with time as more experience was gained. The acquired knowledge was then transmitted from one generation to the next, thus following the basic processes of cumulative cultural evolution and plant gene-human culture coevolution.

Bonsai was first practiced in Japan for personal enjoyment and satisfaction of individuals or their households, mostly by members of the elite, and gradually became known to a broader population. Its cultivation was publicly widespread by the end of the 18th century, and started to spread in the Western world following World War II and the American occupation, with an increase in the number and scope of bonsai exhibitions [65, 69, 70]. As soon as it became more popular, widespread economic interests and trading became a major aspect of bonsai aims and practices, and bonsai evolved from a very personal-traditional position to a significant commercial global value.

Lawns and newly-domesticated ornamental plant enterprises

Lawns, referring mainly to managed grass species, are unique among gardening plants as they are in fact wild grasses that were domesticated and bred quite recently to function as soft-to-hard "green carpets" rather than for their flowers or unique canopy shape. Their domestication and breeding is motivated both by aesthetic values and, in addition, by environmental and social needs. Lawns are used for gardening as patches of green soft carpets in urban neighborhoods, in children's playgrounds, and in a variety of sports activities such as football, cricket, golf and other recreational activities. "Bowling Green" is referred to already in a remote literary source mentioning that "The world's oldest surviving bowling green is the Southampton Old Bowling Green, which was first used in 1299" as mentioned in a manuscript of that period in the royal library, Windsor (71). There is no indication however that the grasses were domesticated, and it is accepted that lawns date initially to the 16th century and are important aspects of the interaction between the natural environment and constructed urban and suburban spaces [72] that became popular with the northern European aristocracy. From the

1860s lawns, mainly for sports, became a middle-class trend and their popularity increased in the US and Europe towards the end of the 19th century. Turf grass revolutionized people's way of living, especially in the urban areas of the more industrialized countries, and are essential to maintaining the urban ecology. As from the middle of the 20th century lawns became a significant industry, and now comprise a considerable part of many urban land areas [73, 74], thus forming another unique niche.

Two additional examples of recently domesticated ornamental plants include several *Alstroemeria* species that are native to South America and were domesticated only during the last 50-80 years and spread worldwide [75, 76] to supply market demands for new attractive cut flowers and pot plants. Wax flower varieties (*Chamelaucium spp.*), that are endemic to South Western and Western Australia, were domesticated recently in the USA and Israel for another reason: their hardiness to dry climates in sunny areas [77, 78].

Unlike rose, tulip and bonsai which are deep-rooted in the cultural history of ornamental plants, lawns, Alstromeria, wax flower and many additional ornamental plants have been domesticated and bred over the last 50-80 years only, as a result of new socio-cultural trends and market demands. Many of them are associated with urban life, recreation activities and environmental concerns. This shift is associated with the increase in personal income, not only of elites but also of broader sections of the society, that enabled more people to spend more money on "luxuries". This has resulted in expanded world markets for new exotic flowers and ornamental plant species. Domestication of grasses to create lawns is clearly the result of socio-economic needs and preferences, and lawns are now viewed as a compulsory element of planning urban landscapes, almost an icon [73].

Aesthetic, symbolic and prestige significance of ornamental plant domestication

Flowers and ornamental plants have attracted people's senses and aesthetic emotions for millennia, triggering the domestication of many species. Over time, especially since

the beginning of the 20th century, they have become increasingly popular in many communities and countries, and thus have become a commercial success. Their world production has surpassed all earlier expectations and they are now grown and purchased by hundreds of millions of people globally. The increasing number of domesticated and bred ornamental plant species, and the modern ornamental plant large-scale marketing system during the last 50-100 years is the result of public interest and a search for additional shapes, sizes, colors, scent and applications – all driven by market demands, human aesthetic considerations, including exotic novelty. In the following we discuss how the aesthetic attractiveness and symbolic assets of ornamental plants became a material marketable asset, and how scientific discoveries and technologies coevolved with aesthetic socio-cultural dimensions of the human niche (Figure 2, Figure 3). To the best of our knowledge this is the first analysis of the role of plant gene-human culture coevolution, human NC and CCE as related to domestication, breeding and global spread of ornamental plants.

Human aesthetics values and senses can trigger specific socio-cultural niches

The earlier claims that aesthetic preferences evolved to enhance survival and reproductive success [79], does not accommodate the cumulative socio-cultural evolution of the aesthetic values of many visual arts, including ornamental plant domestication and breeding. The ongoing domestication, breeding and cultivation of new ornamental plant genotypes fits better with the view that, like other human attributes, aesthetic values are culturally and socially learned from others and further evolve, as they are transmitted and spread to larger communities [14, 16], with preferences being modified by **indirect** and **prestige bias** [14, 80 - 82].

Humans are powerful cultural niche constructors [83], and one such significant dimension of the human cultural niche is the aesthetic dimension that sparked for millennia the arts of painting, architecture, sculpturing and the like. Human aesthetic values have long affected the evolution and domestication of ornamental plants, as is the case with different forms of visual and other arts. In many respects the aesthetic

features of flowers and ornamental plants are similar to those of visual arts such as painting and sculpture. Moreover, the consumers and breeders of ornamental plants make many of the same kinds of choices that visual artists do, i.e., selecting for color, form, size, texture, and pattern, and all are evolving along the principles of cumulative cultural evolution operating within specific transmitted traditions [84]. Thus, the diversity of our individual aesthetic interests and preferences may explain the expanding ornamental plant markets given the fact that the socioeconomic condition permits to spend more money. Once a new variety is exhibited in public, the innovation becomes a social event that can alter the tradition and result in practices like collecting unique "showy" ornamental plants (e.g., orchids, selected succulents and ferns), and gardening exhibitions (Figure 2). The public manifestation results in a specific dimension of human niche that we can term “aesthetic niche” [85]. The market success deriving from the prestige of aesthetic novelty permits the employment of new best practices to progress; once a new form is established **conformity bias** can take over [14, 81]. Indeed, due to adoption of new breeding techniques and marketing strategies, ornamental plant breeders, gardeners and consumers drive forward ornamental plant exhibitions, to enhance the spread of ornamental plants and their popularity, and in addition influence urban environments and communities that they serve by producing aesthetic values, in the form of living plants. For example, competition on prestige and economic value of paintings, sculptures, choreography [84] can enhance public interests and further drive others to produce pieces of arts.

It was suggested that cultivated flowers are rewarding because they have evolved to rapidly induce positive human emotions that can be explained by the personal aesthetic pleasure associated with flowers [32,33]. Beauty is considered to be "in the eye of the beholder"; however, recent studies in neuro-aesthetics indicate in fact that "beauty can be expressed in the brain of the beholder" [28]. Neuro-aesthetics represents a convergence of neuroscience and empirical aesthetics, i.e., the recording of brain responses to aesthetic stimuli [86]. Brain-scanning experiments showed, e.g., that a specific cortical area of the brain was active during the experience of musical and visual

362 beauty [36]. Moreover, it was found recently that oral administration of dopamine
363 modulated and enhanced the reward experiences elicited by music [87]. These
364 examples, and others, may suggest that cultural arts that appeal to human senses, like
365 aesthetic enjoyment of ornamental plants, can be mediated by chemical signals,
366 transmitters and brain activity. Aesthetic values and appreciation of beauty are common
367 to most human beings [30, 31]; however, as we would expect from our cultural
368 evolutionary account, specific differences in what is regarded as aesthetically attractive
369 exist among socio-cultural groups. A study of symmetry, beauty and evolution [37]
370 showed that symmetry preferences may arise as a by-product of the need to recognize
371 objects irrespective of their position and orientation. Indeed, one of the major
372 characteristics of flowers is the symmetrical presentation of the petals which
373 contributes to their attractiveness [88]. It was further proposed that the aesthetic
374 character of personal and group adornment such as jewelry (and for that matter
375 ornamental plants) can promote its function or meaning [85]. It is interesting to note
376 that similar visual characteristics like color were involved also in animal domestication
377 (89) and it was concluded that coat colour most likely appeared very soon after the
378 domestication process began, and that humans have been actively selecting for colour
379 novelty. An alternative view claims that it is not a direct selection of colour but likely a
380 pleiotropic consequence (90).

381

382 *Attractiveness of ornamental plants as symbolic and prestigious marketable assets*

383 The attractiveness of many ornamental plants includes several typical characteristics
384 such as color, scent, symmetry, shape that can have symbolic values in addition to their
385 aesthetic appeal [42]. Colors, for example, often have different meanings in different
386 cultures, and color symbolism is context-dependent [91]. Color symbolism has changed
387 also with time, and colors had in the past also a religious context, e.g., blue being
388 symbolic of heaven and white of purity. Today, purity is still symbolized by white in
389 Australia and the USA, but by blue in other countries like India [92]. Mourning, for

example, is symbolized by white in Japan, black in Europe and the US, and blue in Iran. Accepting the common definition of symbolism, i.e., "to signify ideas and qualities by giving them symbolic meanings that are different from their literal sense", many flowers and ornamental plants function in fact as symbolic assets, e.g., the white Calla lily in funerals and mourning. Moreover, ornamental plants further evolved from functioning merely as aesthetic and symbolic assets to material and practical marketable economic goods. Such is the case with roses where visual aesthetics combined with scent turned it into the world's major cut flower business; with tulips and orchids that became competitive prestige objects for collectors; bonsai trees that originated in Japan and China as a cultural symbolic personal asset, and are now salable goods all over the world.

According to Bourdieu [63, 64], the evolution of society and class differences cannot be explained by economics alone, and cultural assets, which include all types of symbolic goods (e.g., literature and books, paintings, hymns, and also material items like a flag or a myrtle wreath) have two aspects: symbolic and functional. The symbolic assets are referred to as resources available to an individual on the basis of honor, prestige or recognition, and are interchangeable with material goods [63]. Ornamental plants have all these dimensions relevant to social competition [81, 82, 93], and their aesthetic- and symbolic-derived prestige were most likely the road to social and commercial influence [94]. We propose that it is the case as well for flowers and ornamental plants domestication, breeding techniques, cultivation and marketing. The tulipmania period in the Dutch Golden Age is a good example of how a cultivated plant affected the economy and life style, and also vice versa: it indicates how the economic considerations of Dutch merchants, in part due to the desire for economic and social prestige, drove breeders and breeding skills and technologies. The fact that ornamental plant breeding in specific markets is aimed more towards uniformity in flower shape and color, while in others to maximize "eye-catching" divergence of flower colors and shapes, represents a shift in public socio-cultural preferences.

Scientific technologies coevolve with the needs of newly-constructed cultural and social niches

All mentioned domestication and breeding events of ornamental plants could not have been achieved without both the earlier breeding technologies and the current molecular tools used for food plants, that were applied later for breeding ornamental plants. Once a given technology is available, it can be quickly adapted to modify selection pressures in other plants and alter gene frequencies. This raises the question of how scientific discoveries and new technologies, CCE and NC co-evolve [95, 96].

Agriculture is the result of repeated scientific innovations and technologies that are sequentially linked, thus resulting in a chain of progressive innovations [25, 97]. The power of translating novel discoveries in basic sciences to practical applications emphasizes the evolutionary nature and co-dependence of human cumulative culture, scientific discoveries, and technologies that can form successive human niche dimensions. The evolutionary progressive technologies follow the concept that "technology is cumulative… as a result of a process of Darwinian 'descent with modification' " [95]. Moreover, technology evolution is integrated within the concept of all EES elements of ornamental plants – from domestication to market (Figure 3). As proposed earlier [98], the evolutionary entities that are the subject of variation and inheritance include technological lineages, recipes for techniques, and more. This evolution is not necessarily linear; indeed, cumulative technological advances and effects are generally exponential [99]. For example, the basic science of revealing DNA structure [100], was followed later by a series of new techniques for DNA sequencing, recombinant DNA technologies and gene editing in plants, that enabled constructing the large areas of the GM plants niche [97, 101, 102]. Domestication and breeding operations in turn, are additional elements of the Anthropocene [83], that have brought about new socio-cultural questions of food safety, and economic, environmental, ethical and legal considerations [97]. Moreover, the exponential data accumulation of plant molecular studies generated the need to introduce yet other technologies, e.g., machine learning and big data analysis, to enable future studies that were impossible to analyze

without it [103]. The quick adoption and spread of novel plant breeding techniques (e.g., the recent gene editing methodology) precisely follow the reasoning of the cultural evolution theory discussed earlier [14, 82] that is crucial for permitting new best practices to take place (Figure 3).

Technology transfer is another aspect of science-technology-culture coevolution that became more obvious and relevant in the era of globalization, and exchange of methods and technologies now infiltrates most countries and societies [104, 105]. It became an important aspect of the plant industry, for example with respect to availability of cut flowers all year around: specific cultivation technologies that were developed in the Northern hemisphere countries are being transferred to selected Southern hemisphere countries in order to balance the flower market (i.e., shipping cut flowers from Southern hemisphere during the winter season in Northern hemisphere markets). Interestingly, Theophrastus mentioned that roses flowered in Egypt 2-3 weeks earlier than in Greece and were therefore much in demand [106].

Concluding Remarks and Future Perspectives

The extended evolutionary synthesis seems to bridge the divide between biological sciences and human culture, and it is now well accepted that plant domestication is associated with human socio-cultural evolution as studied here for ornamental plants [22-25].

Ornamental plant domestication, characterized by repeated domestication events in various countries and regions, likely follows the protracted domestication process proposed for food plants [107]. The specific case studies studied here comply with the accepted understanding of the extended evolutionary synthesis (and gene-culture coevolution), i.e., that similar socio-cultural norms and motivations for ornamental plant cultivation, in different categories of ornamental plants, can be adopted by different societies in different times.

The human niche cannot be understood without integrating NC with cultural evolution and social change [18, 19].

476 The attractiveness of ornamental plants is both an aesthetic-symbolic and a prestige
477 asset that upon domestication and further breeding became a marketable popular
478 material good.

479 Human culture-driven scientific discoveries and technologies are a prerequisite for
480 improved plant domestication, breeding and large-scale farming, that in turn construct
481 new socio-cultural niches, as shown here for ornamental plants.

482 Finally, the many interactions of human mind and culture, including aesthetic values and
483 reasoning on one side, with new gene and other technologies on the other, results in
484 domestication, breeding and cultivation of both food and ornamental plants - echoes
485 an old Chinese proverb: “When you have only two coins left in the world, buy some rice
486 to eat with one, and a flower for the soul with the other”, as artistically represented in
487 Figure 4.

488

489 Outstanding questions

490

491 Does the new Extended Evolutionary Synthesis theory allow for a better overall
492 understanding of plant domestication in general, and specifically ornamental plant
493 evolution?

494

495 Why were plants domesticated, bred, and intensively cultivated to exhibit new visually-
496 aesthetic characteristics? Is human cultural evolution associated with the expression of
497 aesthetic values?

498

499 Domesticating and breeding of ornamental plants involved over-expression (or

silencing) of specific metabolic pathways (e.g., color and scent metabolites) in response to cultural-social-economic needs – did it enrich our planet with specific alleles, resulting in yet another feature of the Anthropocene?

Ornamental plants have been cultivated since ca. 4,000 BC, considerably later than initial food plant domestication. Did aesthetic values become relevant only at a later human sociocultural stage after the rise of states and the elites, along with craft specialization when material culture evolved?

Acknowledgements

We are grateful to Kevin Laland (St. Andrews University) and Alex Mesoudi (University of Exeter) for valuable comments on a previous version of the manuscript. AA acknowledges Stephen Shennan for hosting him as an Honorary Senior Research Associate at UCL, the long fruitful discussions with Itamar Even-Zohar (Culture Research, Tel Aviv University), and Alexander Vainstein (Hebrew University of Jerusalem) comments on ornamental plants.

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775 **Figure Legends**

Key Figure 1. Components of the extended evolutionary synthesis. The EES includes 3 major inborn and interrelated elements (CCE, NC and GCC), indicating that heredity is not mediated by genes only. Technology Evolution (TE) is a significant outcome of all 3 elements, and together all four pillars interact with each other to express and produce a certain progress or benefit to humanity and/or a novel product (symbolic or material) and/or to the environment (occasionally also negative effects). The relative contribution of each of the 4 pillars is variable, depending on the purpose and end-result. In the case of ornamental plant domestication and breeding: human aesthetic values (CCE) trigger the domestication of a specific plant species, followed by breeding, and the established genotype/phenotype is a manifestation of GCC. Once established in a garden, the ornamental plants confront a new NC (environmental-climatic conditions) that may further modify the genotype/phenotype. When introduced to another country or region, it may undergo a second domestication event due to selecting a specific genotype, and/or responding to people's new local aesthetic preferences and market priorities (e.g., color, shape) - thus a second GCC event. All later breeding and cultivation activities depend increasingly on technology and innovations - the result of CCE. The "Expression of Progress" panel presents various types of "end results", either symbolic or material in: domesticated plants, animals (including In Vitro Fertilization, IVF), and even microorganisms (e.g., "domestication" and isolation of specific yeast varieties for beer production). Additional details in Box 1.

Figure 2. How cumulative cultural and scientific evolution, plant gene-human culture coevolution and newly formed human aesthetic niches drive ornamental plant domestication? The notion that the human sense of aesthetics triggers ornamental plant domestication and breeding is presented in the upper 3 interacting boxes: (1) Cumulative cultural-scientific evolution starts with transmission of accumulated knowledge that results in scientific innovations that are further translated to practical technologies. Scientific innovations and technologies progress sequentially and exponentially to the degree that machine learning has to be employed for data analysis; (2) Plant gene-human culture coevolution, triggered by human sense of aesthetics,

advance sequentially in line with new developing technologies, starting with domestication of natural exotic plants and followed, by traditional breeding and molecular-aided breeding (marker-assisted selection, genetic engineering and genome editing); (3) New aesthetic-driven sociocultural niches are formed , that further evolve depending on personal and group preferences of specific human aesthetic components (e.g., color, scent, symmetry), resulting in the creation of new markets that are regulated by inter-group prestige and competition features. Thus, from being initially domesticated because of their aesthetic and symbolic values, ornamental plants became commodities (4) The resulting plant categories are owned, marketed and bought by consumers because of increased awareness to aesthetic assets, and in part due to social competition

Figure 3. The sequential overall processes of ornamental plant domestication and breeding and its integration with the accompanying technologies. Representation of a "flowering plant" growing from the interacting roots of CEE, GCC, NC and TE (CCE and GCC drive together TE, i.e., technology evolution) that are merged in the EEC root-crown from which the stem and entire plant is growing. The stem is composed of 5 sequential growths "periods" (from the past to more recent). The left-side leaves represent the sequential goals and stages towards marketing the plants, from initial domestication, to phenotype selection, to breeding and genotype selection, to large scale cultivation and marketing. Additional details are presented in the left-side panels. The right-side leaves represent major agricultural and breeding technology-associated phases that correspond to each stage of the left side leaves: early domestication and farming (use of sickles, canal irrigation, ploughs etc.), to the industrial revolution when farming became mechanized, to traditional (including controlled pollination, mutation breeding and hybrid production), to "molecular breeding" (including GM and gene editing), and finally to computerized practices such as machine learning etc. The approximate time period (years) is represented on the right (time when it started; parts may continue for longer periods). The "flower petals" show the specific ornamental plant species discussed here, together with the approximate start of domestication, from the left petals and anti-

834 clockwise: rose to bonsai, to tulip to carnation and gerbera (and many other species),
835 followed by lawns and new landscaping plants, to recently domesticated Alstromeria,
836 Wax-flower and other species, to engineered “Blue Rose” and future engineered and
837 gene-edited ornamental plants.

838 **Figure 4. Origins of the ornamental plant world we live in.** Artistic representation of
839 the interaction between human culture and knowledge (represented on the left by the
840 thinking brain and a book) and plant biology (represented on the right by the DNA helix
841 and flower morphology), that coevolve through scientific-technical advances
842 (represented below by a computer and an irrigation sprinkler) to produce the “target”
843 result, in this case an attractive ornamental plant that satisfies human quest for
844 environmental-friendly aesthetic components (above). Represented is a flowering *Iris*
845 *regis-uzziae*, an endemic wild plant growing in the Negev southern semi-desert, Israel
846 that can be domesticated for both its aesthetic attractiveness being visually-appealing,
847 and as a practical asset that supply market demands. Can it be domesticated? Yes, if we
848 bring together human cumulative culture, genes and cells and technology. If we use, in
849 addition, various breeding technologies to increase, for example, the length of the short
850 flower stalk and to extend its shelf-life, it can become a most desirable marketed
851 rhizome plant.

852 **Box 1. The Extended Evolutionary Synthesis (EES) and its major elements**

853 EES: is characterized by the notion that the direction of evolution need not start with a
854 mutation and does not depend on selection alone. The cause of an evolutionary change
855 may, for example, start with developmental plasticity or niche construction that results
856 in genetic changes. Several developmental processes (e.g. epigenetic effects, regulation
857 of gene expression, construction of internal and external developmental environments)
858 can be involved in the origin of adaptive novel phenotypic variations. Basically, all
859 processes that generate phenotypic variation (including developmental plasticity,
860 genetic, epigenetic, ecological and cultural inheritance) are potential sources of bias [8 –
861 10].

CCE: The evolutionary change in knowledge or behaviour can be horizontal (between members of the same generation), or vertical (from parent to offspring), or both. CCE can result in accumulated ideas and/or new inventions and technologies that selectively accumulate over successive generations. Population CCE is manifested by a sequential series of stages over time: a change in human knowledge and/or behaviour as a result of social learning, followed by transfer of the novel behaviour or knowledge to others, after which the accumulated knowledge results in an improvement or progress of cultural or genetic fitness – all stages are thus repeated and generate sequential improvements over time [14, 15].

NC: is the biological principle that organisms do not just passively adapt to their environments, rather often they actively construct their environments, and those modifications in turn affect their own and other species' evolution. Plant domestication and breeding activities are prime examples of human cultural niche construction, where these practices transform the environment and in turn those environmental changes alter the selection pressures on agriculture. Plant domestication can modify the abiotic environment (e.g., water, salinity, soil composition), the biotic environment (e.g., other plant species, insects, fungi, and weeds), and the social environment (e.g., social norms, regulation, markets) [18, 19, 22, 25].

GCC: relies on CCE, but focuses on cases where cultural inheritance causes changes in gene frequencies, which feeds back on cultural evolution, forming co-evolutionary dynamics. Culturally transmitted processes (including knowledge, inventions and technologies) affect and shape a species' genetic evolution by modifying the selection of genes, and vice versa. GCC has focused initially on functional genes in human populations, and was extended to non-human genes contained within domesticated and genetically modified plants and animals. Plant Gene-Human Culture Coevolution is a branch of GCC, where human culture affects the evolution of domesticated, bred and genetically modified plants genes. [16, 17, 19, 22, 25].

Glossary

Aesthetic Considerations: Aesthetics concerns a large range of disciplines, from art and philosophy to social science, cultural history and physical forms, and thus has different and complementary meanings depending on the field in which it is defined. Aesthetics is discussed here in its common and practical meaning with respect to ornamental plants and gardening (rather than in its philosophical meanings) and adopted by a particular person, group, or culture i.e., those plants which are grown for their beauty, appealing, eye-catching and aesthetic features, in home gardens or in public places like parks; their value relies on their aesthetic appearance, including pleasing flower and/or leaf color, flower and/or leaf shape, fragrance, leaf texture and variegation, and overall plant form or architecture.

Conformist bias: Selective socio-cultural learning of some behavior on the basis that it is the locally most common version. 'When in Rome do as the Romans'.

Cumulative Cultural Evolution (CCE): Cultural transmission of knowledge via social learning from one person and from one generation to another that results in evolutionary change in knowledge.

Extended Evolutionary Synthesis (**EES**): Unlike the earlier "modern synthesis" concept of evolution that merged Darwin's theory of evolution and Mendelian heredity as the sole factors, EES proposes that "there is more to inheritance than genes", i.e., organism evolution in general (including plant evolution and domestication) cannot be explained by genetic concepts only. Rather, it is directed also by physical development, by the environment that shapes organisms' traits, by human socio-cultural processes, and by extra-genetic inheritance that bridge the gap between genetic evolution, the environment and human culture.

Gene-Culture Coevolution (GCC): The ways by which human cultural factors modify and shape their own or other organisms' gene expression and genetic evolution.

Indirect bias: Selective socio-cultural learning of some behavior not on the basis of any intrinsic merit (this would be direct bias) but on some aspect of the individual(s) with which it is associated, e.g. their social status.

Niche construction (NC): The process whereby organisms, through their activities and choices, transform and modify their own and other organisms' environments and niches.

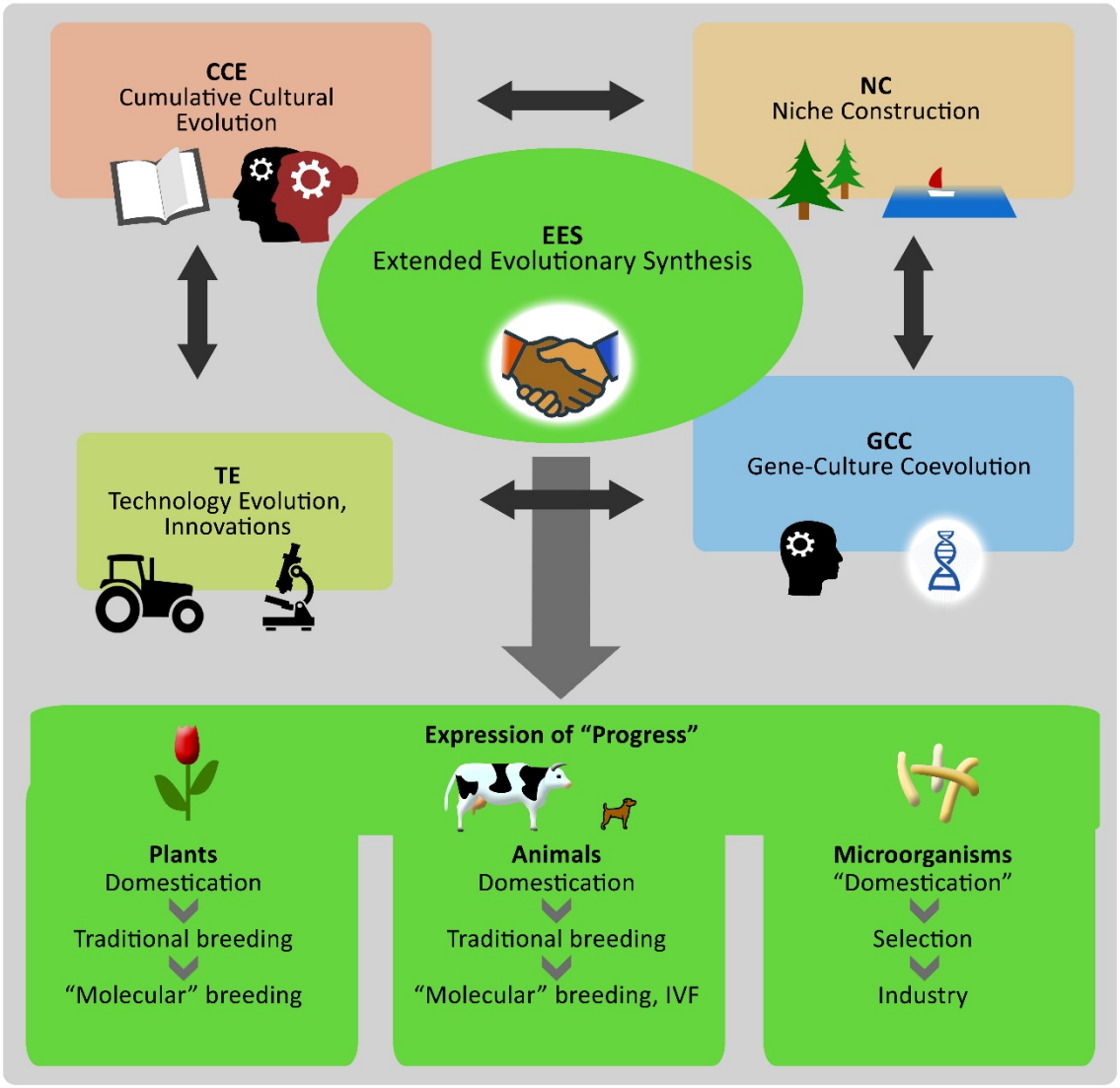
Plant Gene-Human Culture Coevolution (PGHCC): Gene-culture coevolution where the gene is of plants and culture is of human.

Plant Breeding: application of genetic principles to modify plant traits and produce desired characteristics using various technologies (traditional breeding, marker-assisted selection, genetic modification and gene editing).

Prestige bias: Selective socio-cultural learning by copying the behaviours of respected and admired individuals, to attain a high social rank.

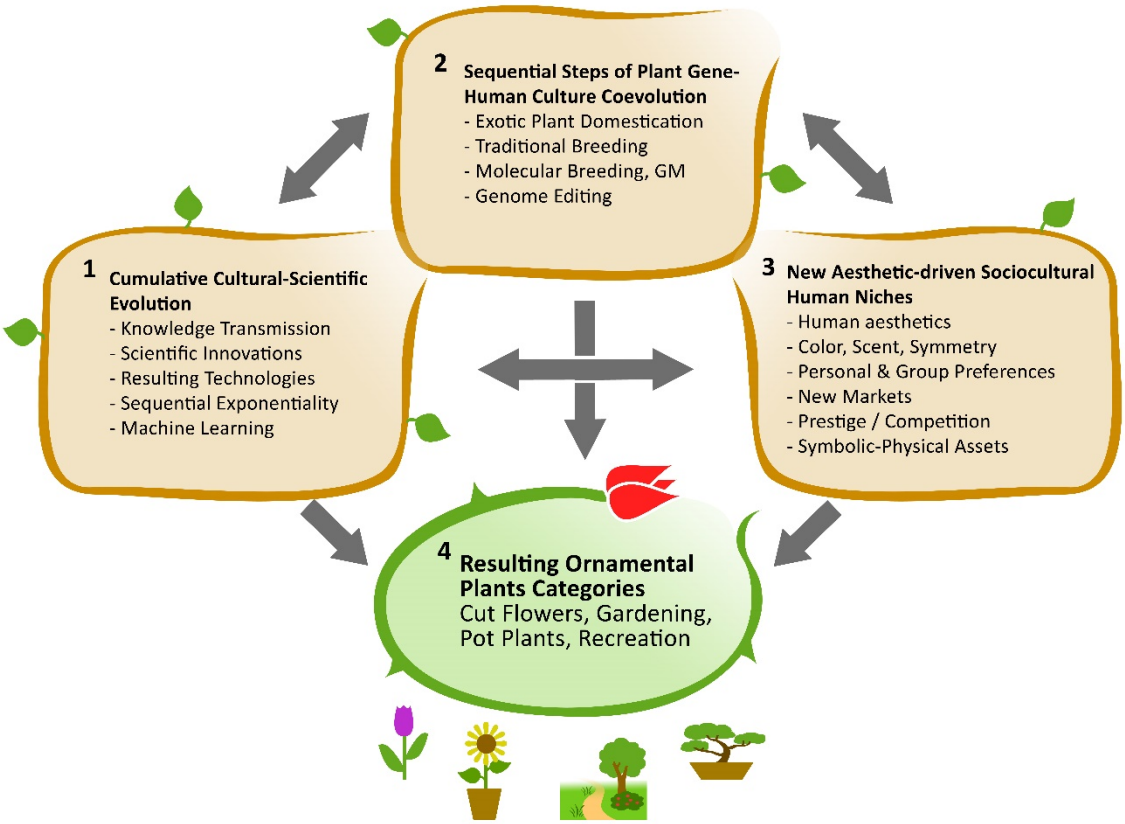
Symbolic Assets/Material Goods: An object, word, or action that stands for something else, something that represents abstract ideas or concepts such as myths, figures, sounds, color, shape, symmetry. Symbolic culture contrasts with material and physical entities, e.g., the color, symmetry, scent of flowers or their use as funeral wreaths have symbolic meaning, but once they are bred, bought and sold in the market they become material goods or commodities.

Tulipmania: was the period during the Dutch Golden Age when introduced tulips rapidly became a luxury item due to intense breeding; contract prices for tulip bulbs reached extraordinarily high levels and then collapsed in 1637, creating a socio-economic phenomenon that rapidly resulted in a significant economic crisis.


CCE
Cumulative Cultural Evolution
NC
Niche Construction
EES
Extended Evolutionary Synthesis
TE
Technology Evolution, Innovations
GCC
Gene-Culture Coevolution
Expression of "Progress"
Plants
Domestication
Traditional breeding
"Molecular" breeding
Animals
Domestication
Traditional breeding
"Molecular" breeding, IVF
Microorganisms
"Domestication"
Selection
Industry

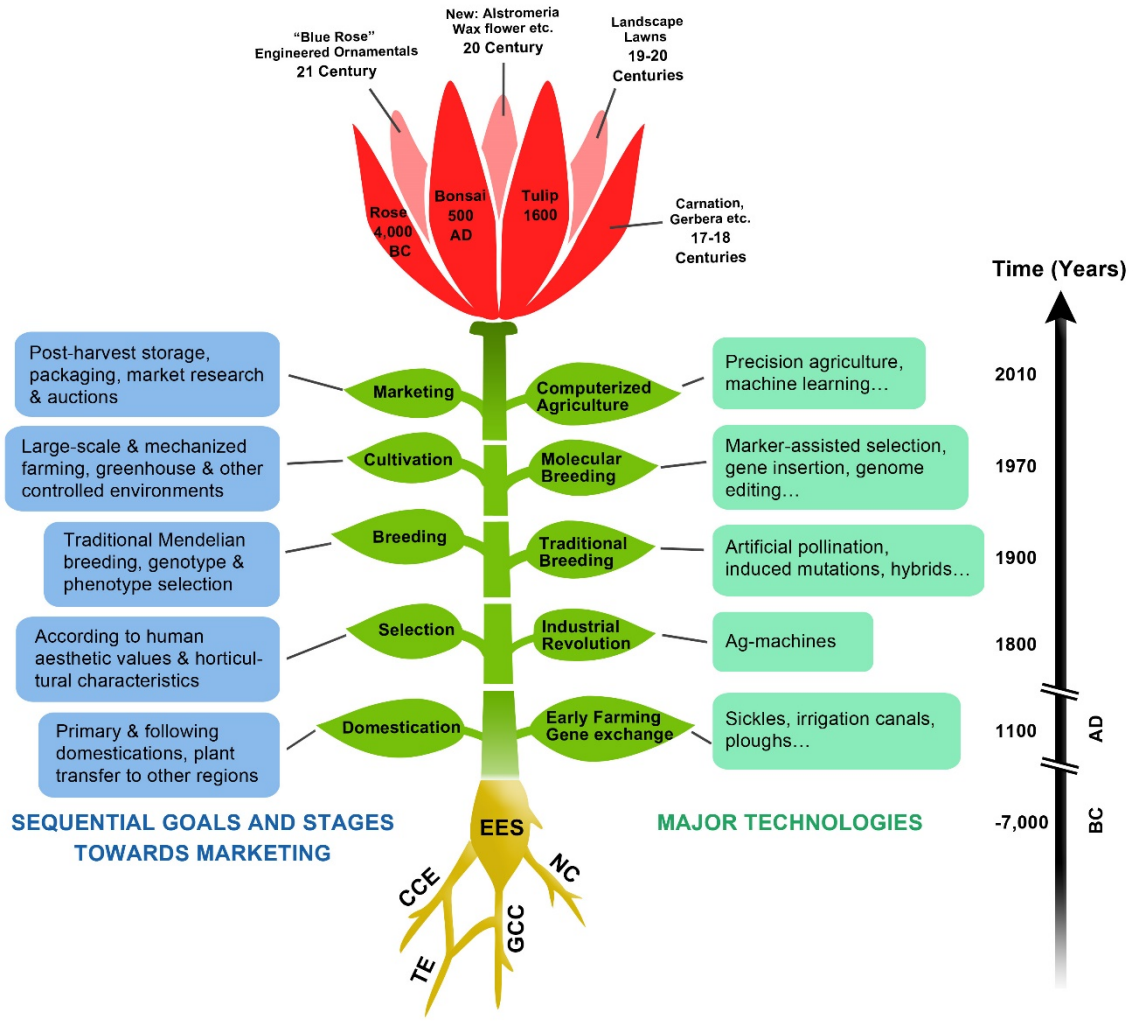
942

943


2 Sequential Steps of Plant Gene-Human Culture Coevolution
- Exotic Plant Domestication
- Traditional Breeding
- Molecular Breeding, GM
- Genome Editing
1 Cumulative Cultural-Scientific Evolution
- Knowledge Transmission
- Scientific Innovations
- Resulting Technologies
- Sequential Exponentiality
- Machine Learning
3 New Aesthetic-driven Sociocultural Human Niches
- Human aesthetics
- Color, Scent, Symmetry
- Personal & Group Preferences
- New Markets
- Prestige / Competition
- Symbolic-Physical Assets
4 Resulting Ornamental Plants Categories
Cut Flowers, Gardening, Pot Plants, Recreation

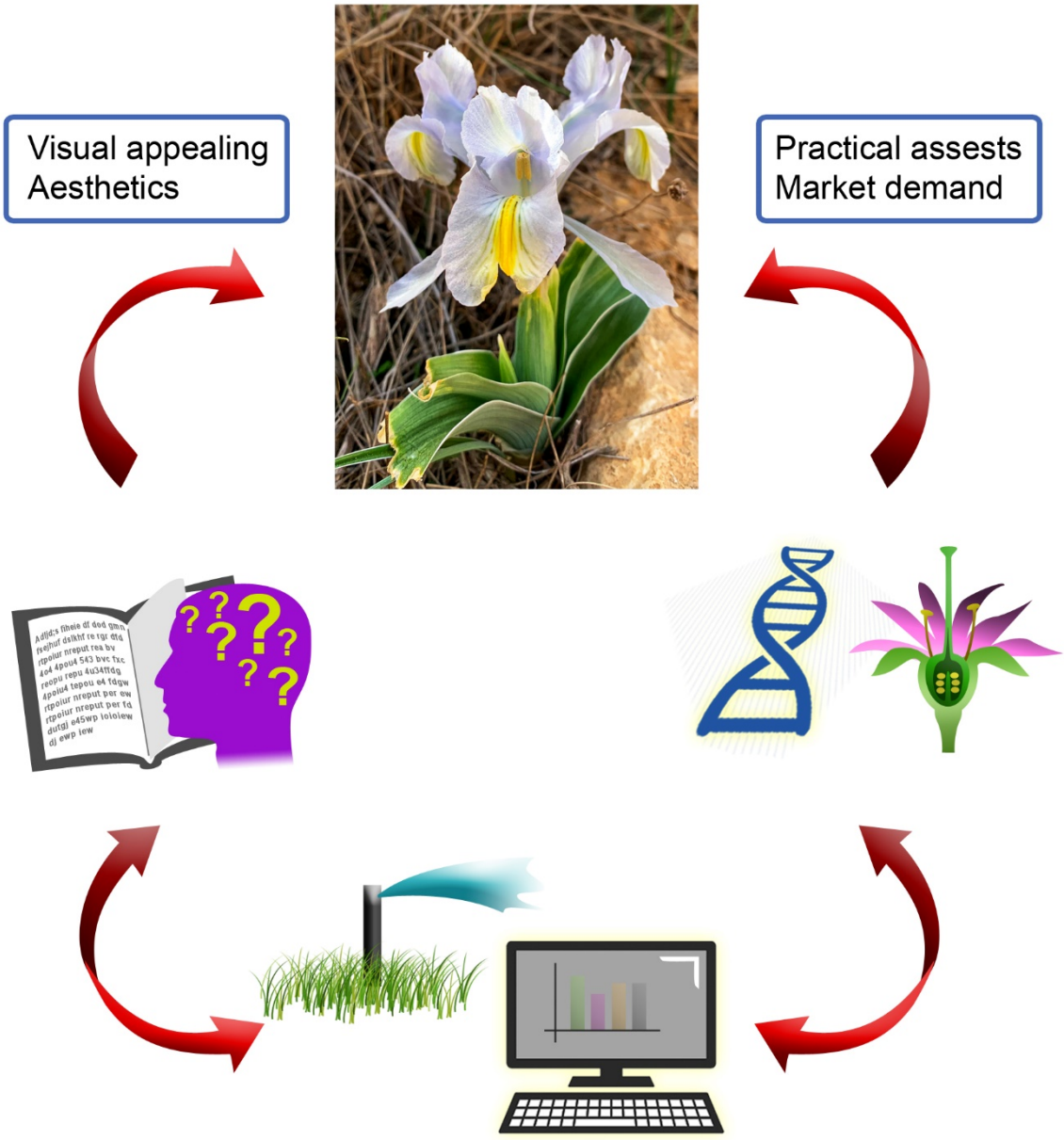
944

945


"Blue Rose" Engineered Ornamentals 21 Century
New: Alstromeria Wax flower etc. 20 Century
Landscape Lawns 19-20 Centuries
Rose 4,000 BC
Bonsai 500 AD
Tulip 1600
Carnation, Gerbera etc. 17-18 Centuries
Time (Years)
Post-harvest storage, packaging, market research & auctions
Marketing
Computerized Agriculture
Precision agriculture, machine learning…
2010
Large-scale & mechanized farming, greenhouse & other controlled environments
Cultivation
Molecular Breeding
Marker-assisted selection, gene insertion, genome editing…
1970
Traditional Mendelian breeding, genotype & phenotype selection
Breeding
Traditional Breeding
Artificial pollination, induced mutations, hybrids…
1900
According to human aesthetic values & horticultural characteristics
Selection
Industrial Revolution
Ag-machines
1800
Primary & following domestications, plant transfer to other regions
Domestication
Early Farming Gene exchange
Sickles, irrigation canals, ploughs…
1100
AD
BC
-7,000
SEQUENTIAL GOALS AND STAGES TOWARDS MARKETING
MAJOR TECHNOLOGIES
EES
CCE
NC
TE
GCC

946

947


Visual appealing
Aesthetics
Practical assests
Market demand

948