



# The Dual Role of Culture in Evolutionary Play: Anthropogenic Expansion Vss Destruction of Biodiversity

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## Abstract

A large number of Green discourse blames the human species for the current ecological crisis. However, this description of humanity as the ecocidal culprit serves to conceal the role of humans, in both past and contemporary pre-industrial societies, as custodians of biodiversity. Indigenous societies are known to have conserved their natural resource base for posterity, by instituting cultural norms and institutions against exhaustive resource use. In addition, pre-industrial societies also increased biodiversity on taxic and genetic levels, by domestication of many wild biota, and on the ecosystem level with agroforestry. While Darwin gave much importance to the process of domestication of plants and animals by means of artificial selection, modern science and agriculture curricula tend to neglect this aspect of the history of human civilization. The novel taxa, created in the process of domestication, are characterized by many morphological and behavioural traits never found in the wild progenitor species. Further selection of favourable traits of the new species created an abundance of distinctive crop landraces and animal breeds.

The increment in diversity at the ecosystem, taxic and genetic levels, by the process of domestication and in ancient agroforestry systems, began to reverse with industrial development over the past two centuries. Indeed, industrial development has been the chief driver of the continuing process of biodiversity erosion and habitat loss worldwide.

Industrial agricultural systems, signposted by the Green Revolution (GR), has severely truncated the on-farm crop species and genetic diversity, which characterised traditional multi-crop farming and agroforestry systems in native agrarian cultures. Over the past six decades, the continual replacement of hundreds of landraces with a handful of GR cultivars, combined with the institutional apathy toward *in situ* landrace conservation efforts, has led to the disappearance of the importance of genetic purity of landraces from breeding programs and heirloom crop conservation discourse. Most of the modern farmers, predominantly dependent on the industrial supply of crop seeds, have forgotten the methods of genetic purity maintenance, resulting in the rapid loss of the hundreds of crop landraces with distinctive properties, which were selected centuries ago for diverse agronomic, gustatory, and aesthetic qualities. A recognition of the value of the custodian role of ecosystem people in creating and conserving biodiversity, vis-a-vis the current industrial decimation of biodiversity on all levels, will likely promote biodiversity conservation ethos in modern societies, and the value of genetic purity of the extant crop landraces.

**Keywords:** Crop Plants; Domestication; Diversification; Genetic purity; Landraces; Selection; Taxa.

## Introduction

It is commonplace to blame humanity as the primal causal factor for the rapid decline of global biodiversity. From the fathers of American conservationism, Gifford Pinchot and John Muir, to the modern urban ‘ecologically concerned’ nature-lovers have advocated protection of wilderness from humans, including what Gadgil (2018) describes as the ‘ecosystem people’. The underlying premises that human civilization in general is anathema to Nature, is strongly expressed in our contemporary popular conservationist David Attenborough, who squarely puts the blame of the current global ecological crisis on the humankind. This positing of humanity and human civilisation against a “pristine” or “virgin” Nature is an old European construct, created to distinguish the ‘West as civilization’ from the rest of the world as ‘savage’ wilderness (Gómez-Pompa & Kaus 1992; Clement and Junqueira 2010; Fletcher *et al* 2021), waiting to be subjugated, tamed, and exploited for human progress. This worldview espoused the metaphorical treatment of Reason, represented in Western thought by civilisation and technology as male, to subjugate and dominate Nature as female (Merchant 1980; Lloyd 1984). The Judeo-Christian ideology of human supremacy over natural world, which existed only “to serve man’s purposes” (White 1967), fitted snugly into Eurocentric worldview, and justified both colonization of the global South, extermination of indigenous peoples in the colonies, and exhaustive exploitation of all natural objects for economic development (Deb 2009a). The unrealistic dissociation of wild ecosystems from “the spiritual, economic, and cultural needs of past and present indigenous and local inhabitants” (Fletcher *et al* 2021: 3) is still prevalent in common thinking and writing about Nature in the global North as well as its ex-colonies. As Ellis *et al*. (2021: 7) write, “Depicting human use of nature largely as a recent and negative disturbance of an otherwise human-free natural world is not only incorrect but has profound implications for both science and policy” – and public education, I would add. The curricular education highlights the prowess of technology to ‘conquer’ Nature, and informs the consequent negative impacts of human activities on

wilderness.

The repudiation of the above depiction of the “negative disturbance of an otherwise human-free natural world” is not to deny the continuing process of irreversible anthropogenic decimation of all wild habitats and biodiversity – a process that has undoubtedly gained an enormous scale and tempo over the past century, in all developed and developing countries. Life’s diversity on the ecosystem, species and genetic levels are disappearing at an unprecedented pace, dwarfed only by that of the Cambrian mass extinction. The enormity of modern techno-urban civilization's impact on biodiversity has espoused a new label for our contemporary age of extinction – the Anthropocene. The widespread description of the subversive agency of human economy in the current global ecocidal process, however, conceals the amazing constructive role of humans in sustaining, and even enriching, biodiversity on Earth over millennia. The notion of human civilisation as the conqueror of Nature has been so deeply engraved in the modern mind that the possibility of human cultures enriching biodiversity by creating new species and ecosystems appears to be “wrong”, and at least uncomfortable to many academics.

## Anthropogenic biodiversity loss and its political economic dimension

That the industrial growth has caused the enormous global output of greenhouse gases and habitat destruction, consequent on global temperature rise and rapid species extinction rates is well acknowledged in both scientific literature and mass media. However, species extinction also occurred before the Industrial Revolution. In this context, the role of past and contemporary pre-industrial societies in extermination of many species by overharvesting has remained controversial. While some authors have shown the aboriginal resource use modes to have transcended the western utilitarian view of nature and served to sustain the resource base for a long time horizon, others repudiate the western Orientalist construction of the ‘ecologically Noble Savage’ (Porritt and Winner 1988; Redford 1991; Buege 1996; Deb 2009a). The latter point out that indigenous societies also eradicated many species in the past. To understand the evolutionary ecological relationship of humankind with the rest of nature, it is necessary to briefly discuss the findings of recent studies in human ecology of resource use, which is in order.

A plethora of studies in the ecological and economic history of traditional resource use systems has established that until the colonial state takeover of forests and wetlands, indigenous societies had protected their natural resource base by various customary rules of governance. The shift of control of local resource base from the hands of local user societies to the state management regime has always transformed the commons into open access resource pool (Ruttan & Borgerhoff Mulder 1999; Oström 2002; Deitz et al. 2003). The ubiquitous pattern of increasing extent of deforestation following nationalization of forests that had earlier been governed by local user groups of ecosystem people, is well documented (Shepherd 1992; Thomson et al. 1992; Jodha 1996; Gadgil and Guha 2013; and many others). Similarly, following the state takeover of in-shore fisheries from local control by the traditional in-shore fishers themselves led to uncontrolled overharvesting (Dasgupta, 1982; Pinkerton, 1989; Cordell and McKean, 1992).

Over the past 300 years, the key factors for depletion of the resources have been (a) the shift of resource governance

from the local user groups to external state agencies, and (b) modern exhaustive technology to enhance ‘economic efficiency’, measured by maximizing resource extraction in the shortest possible time (Deb 2009a). With the rise of industrial capitalism, “nature becomes purely an object for humankind, purely a matter of utility” (Marx, 1857: 269). The logical consequence of this commodification of the natural world and the neoclassical economic institution of positive discount rates, is species extinction and habitat destruction (Bliese 2001; Foster 2002; Petrucci 2002). An instance is the sequence of events that occurred in kelp forests of the Gulf of Maine. Despite intensive aboriginal and early European hook-and-line fishing “for at least 5000 years,” predation by Atlantic cod and other large ground fish kept sea urchin populations small enough to allow persistence of kelp forests. The introduction of new mechanised fishing technology in the 1920s set off a rapid decline in numbers and body size of coastal cod in the Gulf of Maine, extending to Georges Bank. As a result, kelp forests disappeared with the rise in sea urchins due to complete removal of formerly dominant predatory fish (Jackson et al. 2001). The magnitude of losses of marine biodiversity was enormous in terms of biomass and abundance of large animals that are now effectively absent from most coastal ecosystems world-wide; “Their timing in the Americas and Pacific closely tracks European colonisation and exploitation in most cases” (Jackson et al. 2001). New, more efficient extractive technology introduced into native traditional economy also proves to escalate species extinction and habitat destruction. For instance, the introduction of firearms and steel traps to the boreal forest Algonquians of south western Canada in the early 1800s by European fur traders resulted in extermination of wild animals (Burke 2001). Native hunting for millennia had sustained their prey populations, but “only after European contact”, trade replaced group hunting for subsistence of the native societies, and led to extermination of game animals (Burke 2001). In contrast to subsistence hunting by the native Indian hunter-gatherers, ‘game’ hunting expeditions by British officials with their ‘sporting’ rifles spelled doom to thousands of birds and large mammals. Beinart (1990: 164) mentions that during a royal visit to South Africa, six hundred heads of large game alone were shot in one day. Similar single-day shoots killed 4,206 birds in 1916, and 4,273 in 1938, to celebrate the viceregal visits of Lord Chelmsford and Lord Linlithgow, respectively, to Bharatpur (Gee 1965: 35), which is now a large bird sanctuary in India. After the British takeover of all forests and wildlife habitats, the Bengal Florican, dwarf rhinoceros, and the Cheetah became extinct from India. As Callicott and Ames (1989: 280) summarised, “All Asian environmental ills... are either caused by Western technology... or aggravated by it.”

The well documented fact that industrial development as a “super ideology” (Porritt and Winner 1988), with its efficient technologies, enhances biodiversity loss and ecological disasters in all European colonies in the past centuries as well as all ex-colonies (Diamond 1997) is not peculiar to capitalist economies alone (McNeill 2000; Deb 2009a). The drying up of the Amu Dariya and Sir Dariya rivers and the killing of the Aral Sea in the Soviet Union, and the massive deforestation drive in China in the 1960s are the most prominent instances. Globalization of Soviet Union fishing activities from 1950 to 1991 pushed marine fishery exploitation to radically new levels and triggered ecological regime shifts in the Baltic and Black Seas and the Scotian Shelf (Österblom & Folke 2015).

The loss of biodiversity and traditional cultures is a consequence of the urban–industrial mode of land use, economic growth, and market integration (Elmqvist et al. 2016; Brondizio et al. 2019; Sánchez-Bayo and Wyckhuys 2019; Rosin et al. 2020; Deb 2022 and citations there). The industrialisation of agriculture has rapidly truncated agrobiodiversity, escalated deforestation, and groundwater exhaustion in the global South (Deb 2009a). Thousands of native landraces of

rice were replaced with a handful of high yielding varieties (HYVs) within 30 years of the GR (Deb 2017; 2019; Khouri et al. 2021), which also caused severe environmental and health impacts (Pimentel & Pimentel 1990; John & Babu 2021). The replacement of traditional agroforestry and multi-crop farming systems with the GR model of monoculture, combined with synthetic pesticides and herbicides, has caused the local extinction of a large number of broadleaved plants, insects and vertebrates, and drastic reduction in the agorecosystem complexity (Pimentel et al. 2005; Relyea 2005; Deb 2009b; Ito et al. 2020).

## Humans as custodians of biodiversity: Learning from history

In contrast to the modern techno-urban-industrial *homo oeconomicus*, most of human societies in the past millennia used to conserve their resource base for long term use, and enhanced species and genetic diversity, which still constitute the basis of production economies. There are hundreds of contemporary pre-modern societies that still remain largely ignorant or incapable of modern technology that is geared to exhaust natural resources, destroy natural habitats, and pollute the environment, both locally and globally. The Akuntsu and the Awà of Brazil, the Jarawa of the Andaman islands, the Hazda of Tanzania and the Menominee of Wisconsin, USA have not pushed any species to extinction, despite the history of their hunting-gathering and fishing economies over millennia. Continual hunting by early humans caused species extinction at many places in the past – for instance the elimination of sea cows from most of their range in northern Pacific plausibly by aboriginal hunting in the early Holocene (Jackson et al. 2001). Nevertheless, wasteful hunting and gratuitous exploitation of resources seldom took place in traditional hunter-gatherer societies in the past, and there is enough evidence to suggest that most of the past as well as contemporaneous pre-industrial societies have learned from their past profligate resource use modes, and learned to conserve their resource base, by instituting cultural norms against exhaustive resource use (Callicott & Ames 1989; Gadgil and Guha 2013; Gadgil et al. 1993; Berkes 1999; Berkes et al. 2000; Deb & Malhotra 2001; Deb 2009a; Nitah 2021). These mutually agreed social and cultural sanctions and restraints on resource use constitute what Gadgil calls "ecologically prudent resource use rules" and Oström (1990; 2002) terms "rules of governance of the commons". Sacred species, sacred groves and seasonal restrictions on hunting and fishing are prominent examples of ancient cultural institutions for the protection of local resource base (Deb & Malhotra 2001; Sheridan & Nyamweru 2008; Deb 2014). The last surviving populations of several rare and endangered endemic taxa are still found in sacred groves and ponds in Asia and Africa (Deb 2009a; 2014; Gadgil 2018).

In addition to preserving the stock of bioresources for their own survival, and for future option value (Deb 2014), indigenous societies are known to have expanded the spectrum of biodiversity by enriching local ecosystems. The most prominent testimony is the Amazonian rainforest, imagined by the West for centuries as "pristine" and "virgin". Recent research shows that this enormously speciose, complex ecosystem is a result of Mayan polyculture agroforestry over thousands of years (Gómez-Pompa & Kaus 1992; Raffles 1999; Lombardo et al. 2020). Another example is the forest-savanna mosaic in Kissidougou of Guinea, which was described in colonial forestry literature, school textbooks, statutes of environmental NGOs and international conservation agencies as well as all administrators and environmental policy-makers for two centuries as the relic of an ancient climax forest, degraded by centuries of logging, shifting cultivation and



bush fires. Groundbreaking research by Fairhead and Leach (1996) has shown that these so called 'remnant forest islands' of Kissidougou are more accurately post-savanna than post-forest: The forest mosaics are not degraded, sub-climax vegetation, but were created by native people who had been planting trees over centuries (Fairhead & Leach 1996).

Early Holocene humans also enriched biodiversity by adding novel taxa (species, subspecies and landraces/ breeds) to the list of life forms on earth. Every domesticated species – plant or animal – is a new species or subspecies that never existed before domestication (Darwin 1868). The domesticated biota were created by artificial selection and breeding of wild ancestral species over many generations. This selection process was understood by Darwin as equivalent to the process of species creation by means of natural selection. Darwin's revolutionary world view explained the origin of different species by means of 'selection' of variants among groups of organisms of common descent (Darwin 1872). The process of artificial selection by humans was to him an important evidence to the workings of natural selection, for which he collated enough evidence in *The Variation of Animals and Plants Under Domestication* (Darwin 1868), published four years before the last edition of *The Origin of Species* (Darwin 1872). Darwin noted the importance of the arduous process of anthropogenic creation of new species (*ibid.*, p. 3): "No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring. But the initial variation on which man works, and without which he can do nothing, is caused by slight changes in the conditions of life, which must often have occurred under nature. Man, therefore, may be said to have been trying an experiment on a gigantic scale; and it is an experiment which nature during the long lapse of time has incessantly tried. Hence it follows that the principles of domestication are important for us." Yet in the next century, this "principle of domestication" went out of sight of the mainstream biology curriculum at schools and universities in many countries. Likewise, domesticated animals and crop plants seldom find mention in popular description of biodiversity.

## Domestication of biota: Expanding taxic and genetic diversity

The first domestication experiments began by taming the Eurasian grey wolf (*Canis lupus*) and breeding them by selecting different characteristics of preference of Pleistocene humans, more than 14000 years before present (YBP), to create *Canis familiars*, the dog (Morell 2015). Domestication of a few food plants also began in the Mesolithic, and continued after the Iron Age. Annual or biennial herbs were preferred for domestication, because perennial trees take very long time to grow, and not useful for farming (Diamond 1997). A series of domestication experiments were successful with pig, goat, sheep, cattle, water buffalo, horse, donkey, camel, llama, yak, and fowl, alongside a plethora of novel crop plants that expanded the diet spectrum of modern humans (Ucko & Dimbleby 1969). An illustrative list of domesticated animals is given in **Table 1**. The onset of Agricultural Revolution, begun between 10,000 and 12,000 YBP, is characterized by cultivation of all domesticated plants, some of which are listed in **Table 2**.

Because dog-wolf hybrids are fertile, older authors considered the dog as a subspecies of an extinct lineage of Eurasian wolf (*Canis lupus*). However dogs who become feral such as the dingo in Australia do not turn into wolf. The biological species definition, based on fertile hybrids, is often inadequate because it is inapplicable to many plants where polyploidy

leads to diversification of species (Darlington & Janaki Ammal 1945). Even among animals, some interspecific hybrids are fertile. The ubiquitous fertility of the hinny, which is a cross between a stallion (*Equus caballus*) and a female donkey, a jenny (*E. asinus*) does not indicate that the two parents belong to the same species. Furthermore, distinctive hematological differences have been found between mules and hinnies (McLean et al. 2016). Whether the domesticate is a new species (such as *O. sativa*) or a subspecies (e.g. Emmer Wheat (*Triticum turgidum* spp. *dicoccum*)), it is evident that the taxon had never existed in nature until the process of domestication created them. Thus, the creation of new species and subspecies imply an enrichment of biodiversity on the taxic level. In addition, the diversity of landraces contribute to genetic diversity of the domesticated species. The landraces and breeds of the domesticates highlight certain novel traits that are absent in the progenitor species (see below).

## The conditions of domesticability in animals

Domestication is beyond the taming of wildlife, and a domesticated animal is a lot more than a pet. There are ample historical records of taming of peafowl, swan, elephant, tiger, cheetah and several species of deer, and keeping them as pets, in ancient Egypt and India. However, the genomes of all these animals remained unaltered, and no new species or subspecies came off their stock. The process of domestication, however, alters the genomes of the wild progenitor species, and involves a few distinct steps. The first step of the domestication process is based on the relationship of a phenotypically plastic organism habituated to human presence, and occurs before any genotypic change; therefore, it can last a long time. This process is called the Baldwin effect, consisting of an evolutionary transition from a facultative tolerance to humans toward a dependence on them (Crispo 2007). During this transition, the animal population becomes accustomed to human association and a strong selection for docility in the animal shapes its behaviour (Yacobaccio 2021).

Selection and breeding of the selected progeny from the progenitor stock is essential for creating a distinctively different domesticated species or subspecies. Many breeds of domestic animals, such as the Mexican toy dog Xoloitzcuintli, are mostly incapable of living in the wild. Another example is the domestic silkworm, *Bombyx mori*, whose ancestral species, now extinct, was the common ancestor of *B. mori* and the wild silkmoth *B. mandarina* (Yukuhiro et al. 2002). While most of the genes of the ancestral species are retained in the extant silkmoth, it cannot survive in the wild. However, *Samia cynthia*, the progenitor of the only other domesticated silk moth *Samia cynthia ricinii*, still survives in the wild in India and Thailand. By contrast, the honey bee (*Apis mellifera*) can forage and survive in the wild, because it has never been properly domesticated (Oldroyd 2012). Indeed, humans have learned to manage this bee for 7000 years — “albeit in sophisticated ways — by providing them with artificial hives, and sometimes also providing them with sugar solution as a substitute for nectar, to rob them of their honey and wax.”

Larson and Fuller (2014) surmise two alternative pathways of animal domestication: Some animals were attracted and took advantage of the human niche, including human food waste, and were eventually habituated to the human habitat and later became commensals, “at which point the establishment of a reciprocal relationship between animal and human would have laid the foundation for domestication, including captivity and human-controlled breeding” (p. 117).

Alternatively, intensive exploitation of large- and medium-sized prey animals led to capture and herd management strategies by early humans, leading to the domestication of these populations. From this perspective, domestication is “a way of greatly increasing the exploitation of species that have long been our prey” (Larson & Fuller 2014: 107) This obviously does not apply to the domesticated crop plants.

After domestication, the animals become distinctly different from their wild ancestral species in four ways:

- a. A continuous supply of eggs and/or flesh and/or milk or wool from the animals every generation can be ensured by repeated breeding (iteroparity) of the animal. This primary economic imperative of food security in every generation was the principal drive for domesticating an animal, which must either breed frequently or (for small animals) have a large litter size. Furthermore, the need to secure food availability during periods of water and fodder scarcity led to restraint of the animal’s natural breeding – by castration, or by prohibiting mating of the animals (see below).
- b. The diet spectrum of the domesticated species is modified by replacing their natural diet with predominantly “unnatural” food items provided only by humans: for instance, domestic cats and dogs can be fed on cooked vegetables, fruits, yogurt, etc., while cattle, goat and sheep can be fattened by feeding on cooked rice, barley, millet, oil cake, transgenic soya (as in the US), and even powdered animal flesh, as used in the UK beef industry, that served to spread the Mad Cow disease (IRTA (2019). It appears that the greater the advancement of domestication, the farther the animal is pushed away from its natural diet base. Of course the domesticated carnivores have not lost their innate ability of hunting prey animals, but the point is that they remain healthy on human provision of processed foods like cooked potato and yogurt in captivity – which the gray wolf and the jungle cat could not.
- c. Domesticated animals do not need the privacy of a wild habitat for breeding; dogs mating in the street and cattle mating in pasture fields are a common sight. As the famed archaeologist-poet, Stuart Pigott (1969) poignantly informs in his South American Idyll:

*The courtship of the llama*

*Embarrasses the farmer*

*But it copulates far sooner*

*Than the kinkier vicuña.*

In contrast, the preference of seclusion and different behavioural traits of individuals tend to limit the success of reproduction of wild mammals in captivity. The classic case of a Sumatran tiger killing his intended mate in London Zoo indicates that a careful choice of “perfect mates” based on genotypic matching is not enough for mating in captivity (MacDonald 2019). Difficulty of breeding in many mammals are reported in zoo literature. Typically, for giant panda in captivity, “Even a female in heat rarely elicits a response from a captive male panda.” Some studies indicate that “giant pandas breed most successfully when they’ve had direct physical contact with keepers, as well as access to climbable trees and private areas away from public scrutiny” (Engber 2005). Because the reproductive behaviour of individual animals is governed by a whole range of phenotypic traits, including intraspecific social interactions, an emphasis on genotypic matching between the mating pair is not enough to ensure breeding success (Kaumanns & Singh 2015). The



neolithic humans who had domesticated animals were careful to select the important phenotypic traits of the wild ancestral mammals in captivity, and bred them to not mind the absence of “private areas away from public scrutiny”.

- d. When released from human association, a domesticated species may become feral, which nevertheless is distinguishable from its wild relatives and extant ancestral species: feral dogs (e.g. dingo) resemble, but do not turn into the wolf, any more than maize seeds strewn in a forest turn into teosinte after umpteen generations.

Neolithic humans domesticated only those animals who expressed the above four primary “domesticable” traits. In other words, the animals that had not evinced these traits in early stage of domestication, were not domesticated. Thus, horse (*Equus ferus caballus*) was domesticated in the Pontic-Caspian steppe from an extinct ancestral species (Olsen 2006), and donkey (*E. africanus asinus*) were domesticated from the ancestral stock of *E. africanus* (Kimura et al. 2011), but none of the Grevy's zebra (*Equus grevyi*), plains zebra (*E. quagga*) and mountain zebra (*E. zebra*) could be domesticated. Similarly, gazelles were never domesticated (Zeder 2006), although Near Eastern gazelle hunters in the Epipaleolithic period practiced a game management strategy to avoid culling reproductive females to promote persistence of the gazelle population (Rowley-Conwy & Layton 2011).

After domestication, the methods of management of the livestock involved the control of the animal's reproduction, in order to restrain free and promiscuous breeding of the domesticates, especially if harsh environmental conditions reduce the progeny's survivorship. The Tuareg arrange for the kids of their goats to be born in two distinct seasons, contingent on the expected availability of pasture, so as to spread the availability of milk yield over most of the year; and they bind “the prepuces of the he-goats and rams which are not to be allowed to breed.” (Cranstone 1969: 254-5). The Nuer castrate all the bull-calves except one from the best milk-yielding cows for breeding. Pastoralists also castrate their cattle, horses and camels by either removing or damaging the testicles – in order to make the animals larger and more docile (Cranstone 1969). Thus, selective breeding of the animals for more yield of milk, meat or wool resulted in the creation of diverse breeds, radically different from the progenitor species.

## The genetic bottleneck vs novel traits in domesticates

Understandably, domestication entails a curtailment of the genetic diversity of the wild progenitor species. When only one allele of a gene is selected for successive breeding experiments, all other alleles of the gene are eventually ‘selected out’ from the progeny. The intensive selection of non-shattering trait in the first domesticated rice led to the loss of the allele responsible for shattering of grains in all the domesticated progeny. However, the varying degree of threshability – ‘easily threshed’, ‘moderately difficult to thresh’ and ‘difficult to thresh’ – demarcate different genotypes of different landraces. The diversity of certain genes is not lost altogether when several landraces are selected for multiple phenotypic traits. For instance, the different genes and their alleles governing the presence of long awns, purple culm and early maturity in the wild rice are retained in different cultivated landrace populations, characterised by the presence of those characters. Hundreds of rice landraces evince a wide range of pericarp colour (white, ivory, green, light brown, red, reddish purple, purple and black), governed by different genes and their alleles present in both *O. rufipogon* and *O. nivara*. Most of the

ancestral genes are still retained by the domesticated silkworm, as mentioned above.

The loss of many wild ancestral traits is almost always accompanied by “some new combinations of old characters”, resulting essentially in new taxa, as elaborated by Darwin, and later by Davenport (1910). The curled tail and the droopy ears of the dog breeds and Belyayev’s fox are prominent examples, never found in the progenitor species. A similar ‘domestication syndrome’ is the architecture of panicle in domesticated rice (Li et al. 2006 a), never found in the wild progenitor species. Another such novel genetic acquisition in domesticated rice is stickiness (when cooked) in some *japonica*-type landraces. The stickiness is conferred by a nucleotide substitution that affected the function of the *Waxy* gene that encodes a granule-bound starch synthase, leading to the reduction of the amount of amylose in the endosperm (Sang & Ge 2007).

New alleles and novel allelic combinations also may arise from on-farm selection of traits from crop landrace populations under different environmental conditions. A 26-year long experiment with bread wheat (*Triticum aestivum* L.) by the French National Institute for Agricultural Research (INRA) revealed that different climatic conditions had elicited divergent selection on flowering time. In two of three environments studied, “the emergence of new alleles that were not detected in parental lines was identified” (Bellon et al. 2017: 968).

## Conservation consequence of domestication

The fact that much of the genomes of several species now extinct are preserved in their domesticated progeny may indicate that domestication have incidentally conserved at least part of the ancient genomes of the extinct progenitor species of, for instance, modern horse, cow, sweet potato and wheat. In addition, several naturally evolved species are nearly extinct in the wild, and currently exist predominantly as domesticates, as instanced by the Syrian hamster (*Mesocricetus auratus*) (Gattermann et al. 2001). Despite the 7000 years’ history of exploitation by humans, the European honey bee (*Apis mellifera*) remains wild (Oldroyd 2012).

Aside from direct economic utility, cultural and religious values also have encourage domestication, leading to conservation of several biota. The sacred basil (*Ocimum tenuiflorum*), for instance, is ritually planted in millions of Hindu households in India, but is scarcely found in the forest (Deb & Malhotra 2001); the major reason of its decimation in the wild is the colonial silvicultural practice since the 1860s, in which all “minor species” were eradicated to promote the growth of commercially valuable timber species in native forests (Deb 2014). Several rice landraces are ingredients of recipes for specific cultural and religious ceremonies, which used to encourage the continuation of their cultivation (Deb 2021 a; 2021 b).

## Selection and amplification of traits in domesticates

The first domestication of rice began when the first unknown, unnamed Neolithic innovators identified and selected the sessile, non-shattering grains of the ancestral *Oryza rufipogon* plants some 12,000 YBP. While ‘shattering’ of seeds in all

wild cereals is an efficient mechanism to enhance seed dispersal and germination success, the selective loss of this property ensures loss-less harvest for consumption (Li et al. 2006 *b*). Subsequent breeding experiments focussed on other important characters such as longer panicles (more edible grains), bolder and heavier grains (more starch) and basmati-like fragrance, imparted by 2-acetyl 1-pyrroline. These novel genetic traits demarcate several domesticates either as a new species or a subspecies of the progenitor species. Although gene exchange still occurs between the ancestral *O. rufipogon* and the cultivate rice *O. sativa*, the latter remains a distinctly new species, just as bread wheat and maize are taxonomically new species, distinct from their progenitor species. The first farmers who had selected the non-shattering mutation in ancestral wild rice population, and those who had identified the high storage potential of starch in wild teosinte and began the process of domestication to create *Oryza sativa* and *Zea mays* respectively, were highly talented individuals with keen powers of observation and farsight. I prefer to recognize these early innovators as unknown and unnamed farmer-scientists, who expanded the food repertoire for today's humanity.

The process of domestication of a species from the ancestral stock is lengthy. Early farmers selected several traits (e.g. the loss of seed dormancy, loss of shattering, increases in seed size and changes in reproductive shoot architecture) during the initial transformation and establishment of the new domesticated species or subspecies. The collection of novel phenotypic traits associated with the genetic change in a domesticated form of a plant, distinct from its wild progenitor, constitutes the domestication syndrome, which includes grain retention (as seen in rice, barley, wheat, soybean), reduction of lateral branching (as noted in maize, sunflower), or modification of flowering-time (as seen in sunflower, maize, soybean). Archeological and genomic studies reveal that domestication traits may often overlap with diversification traits, which arose from "variations in domesticated populations, as they result from crops that are adapting to fit specific uses, preferences and ecological growing conditions" (Meyer & Purugganan 2013: 843). The genes involved in early domestication contribute to various traits, such as inflorescence development (*Brassica oleracea* *CAL*; common bean *TFL1*), vegetative growth habit and plant height (maize *tb1*; and rice *PROG1* and *LG1*), seed pigment, seed size, ornamentation (rice *BH4*; barley *NUD*), and maize teosinte glume architecture1 (*Tga1*), seed retention (rice *SH4-1*; sorghum *SH1*) etc.

Human-directed selection accounts for the initial appearance of traits that differentiated wild and domestic phenotypes (Larson & Fuller 2014). The famous experimental study in animal domestication of Dmitry Belyaev with farm foxes showed that tameness of an animal was a critical factor in the domestication process, which elicited several prominent anatomical and physiological changes in the domesticate. Belyaev carefully selected only the tamer individuals of the silver fox in his domestication experiment that continued for more than 40 generations, and bred individuals who wagged their tails when they were excited, sniffed and licked their caretakers. Eventually, the foxes' tails became curly, ears became floppy, and the shape of their skull and jaws changed (Goldman 2010). This experimental recreation of the "domestication syndrome" demonstrated that several novel traits in the domesticated fox were "not only never seen in wild progenitor species, but also had never been directly selected for" (Larson & Fuller 2014: 117).

The modern horse (*Equus caballus*) belongs to a lineage called DOM2, which is genetically different from all the wild horses including *Equus ferus*, *E. przewalskii* as well as the tarpan horse. Instead, it was bred from a domesticate in the western Eurasia steppes in the late fourth and early third millennia BCE (Librado et al. 2021). Aside from a novel genetic

variant leading to docility of the animal, a unique locus “peaked immediately upstream of the *GSDMC* gene, where sequence coverage dropped at two L1 transposable elements in all lineages except DOM2”. These L1 insertions remodelled the DOM2 gene structure that relieved the animal from chronic back problem. This novel genotype led to the selection of horses that were “involved in new locomotor exercise, including endurance running, weight bearing and/or warfare”(Librado et al. 2021).

## Artificial selection and post-domestication diversification

Upon creation of each new species, selective breeding of variant individuals with different sets of morphological characters led to the creation of diverse varieties/ breeds/ landraces. N.I. Vavilov collected more than 250,000 unique samples of crop landraces from five continents and identified Centres of Crop Diversification where, he surmised, ancient farmers had developed those landraces *post-domestication* (Hummer & Hancock 2015). Hybridisation of wild species and their natural variants also led to the creation of novel plants, whose signature is in polyploidy (Darlington & Janaki Ammal 1945). An example is the Java ‘citronella grass’ – the tetraploid race of *Cymbopogon flexuosus*, “which is evidently a hybrid between the diploid and hexaploid”, and “occurs only as a cultigen” (Janaki Ammal 1951). While most of the crop landraces were created by means of selection of traits (or “the initial variation” *sensu* Darwin) already present in the wild ancestor, some ‘diversification genes’ (such as the rice *LG1* gene, associated with a closed panicle trait) seem to be novel alleles in domesticated landraces that are absent in the wild progenitor species. The selection of either old or novel mutants during the diversification stage contribute to a range of phenotypes, including fruit shape and size (tomato *FW2.2*), inflorescence architecture (barley *VRS1*; soybean *TFL1B*; and maize *Sos1*), starch composition traits (maize *sugary1* (*su1*) and *WAXY* in multiple species), fragrance (rice *BADH2*) and pod corn (maize *MADS19*), etc. (Meyer & Purugganan 2013). The last three traits were selected for specific cultural practices and preferences, rather than for yield enhancement or adaptation to physical environmental stresses.

A thin body of modern research explicitly recognizes the role of local farmer communities in shaping the genetic architecture and biodiversity of the cultivated plants. Intensive breeding and selection by ancient farmers led to different potato landraces with increasingly reduced amounts of harmful glycoalkaloids, longer-day photoperiod sensitivity, and larger size (Hardigan et al. 2017; Siqueira et al. 2023). Intensive breeding of barley by ancient farmers caused the differentiation of hull-less barley and 6-rowed phenotypes from wild ancestors and made them genetically unique (Dai et al. 2012). The very name quinoa in the Quechua and Aymara languages means ‘Mother Grain’, which was historically an important food grain for ancient Andean people, who subsequently selected and bred diverse genotypes of the plant, such as the salt and drought tolerant landraces (Bazile et al. 2013). Farmers of eastern India selected and developed several rice lines with hard and long awn on the rice grain as a defensive adaptation against grazing animals, while coastal mangrove farmers of the Sundarban deltas developed several salinity tolerant landraces or folk varieties (Deb et al. 2005; Deb 2019). Long grain, bold and heavy kernel, high panicle density, high frequency of productive tillers and related morphological characters were selected in hundreds of locally-adapted rice landraces for direct yield benefits. Folk crop varieties are fine tuned over centuries to local soil and climatic conditions, and many of them can outperform modern

cultivars in marginal environmental conditions (Cleveland et al. 1994; Deb 2017; 2019). In addition to the direct economic value, gustatory and aesthetic preferences were also a driver of post-domestication selection of several morphological characters in folk crop varieties (Deb 2017).

It behooves to denote the term 'landrace' I employ here. From a medley of definitions of landraces (Zeven 1998), I adopt the description by Teshome et al. (1997), as "variable plant populations adapted to local agroclimatic conditions which are named, selected and maintained by the traditional farmers to meet their social, economic, cultural and ecological needs." Into this definition, I incorporate Louette et al.'s (1997) definition of a "farmers' variety" which has not been improved by a formal breeding programme. A connotation of landrace is that it is a locally developed folk variety that has been grown in an area for many years or has been selected from varieties long used in the area, as described by Dennis (1987) and Deb (2017). Although this term is mostly applied to crop varieties, it can be also applied in the same sense to 'breeds' of domesticated animals.

Post-domestication selection in animals also created novel variants, such as body size and coat colour in animals. The curled tail for example is a novel trait that evolved upon domestication of the fox in Belyayev's experiment (Goldman 2010). In Bunny rabbits, "telltale changes in coat color weren't documented until the 1500s, when domestication was in full swing. Skeletal changes, like differences in size, didn't come about until the 1700s, when pet breeding began." (Wei-Haas 2018).

Heritable phenotypic changes across generations may also result from differentially methylated alleles, linked to some agronomically important traits (Miura et al. 2009) Aside from the genetic differentiation of the domesticated biota directed by artificial selection, epigenetic alterations could promptly respond to environmental signals independent of genetic bases. Epigenetic changes might partially account for phenotypic adaptation to the rapid artificial selection in *Bombyx mori* (Xiang et al. 2013).





**Fig. 1:** A Glimpse of Rice (*Oryza sativa* ssp. *indica*) Genetic Diversity: showing rice grains (top row) with diverse awn size and colour (labelled **d**), (e), and (i); extra-long sterile lemma (**h**); and kernels (bottom row) with notched belly (**c**), black kernel (**e**) and double-kernel (**n**). [Photo: Author]

## The significance of genetic purity of landraces

Traditional rice farmers of India selected certain exceptional traits and developed pure lines with such traits as fragrance, double-kernel grains, grains with extra-long sterile lemma and embryo-shaped kernels with notched belly (**Fig. 1**) – purely for aesthetic preferences, with no obvious agronomic dividends (Deb 2017; 2019). The genetic bedrock of these traits, which constituted what Darwin called "the initial variation" inherent in the ancestral population, was selected and amplified in pure lines of specific folk varieties. After a stable association of perceptually distinct phenotypic characters demarcate a landrace. Traditional farmers tried to maintain its genetic purity over generations, based on several phenotypic characters which they distinguished – such as aroma, purple node, long awn, red pericarp, submergence tolerance, salinity tolerance, etc. In specific landrace populations, self-pollination increased to release homozygotes, with certain homozygous genotypes producing favourable combinations of recessive genes to form different varieties (Oka 1994). For instance, every pure line aromatic rice landrace is characterised by the homozygous recessive *BADH2* alleles (8 bp deletion in exon 7 and C/T SNP in exon 13) in each grain (He et al. 2015). Thus, a "pure line" of an aromatic landrace must inherit two copies of the 8-bp deletion in the gene. If a proportion of this population is heterozygous for this allele, the grains will become aroma-less, indicating the loss of genetic purity of the landrace. Just as in selecting animals domesticates, ancient breeder carefully selected the phenotypes of individual plants rather than their incidental genotypic contents. The view of individuals as "gene carriers" alone (Kaumanns & Singh 2015) needs to be altered while handling

real-life populations.

Traditional farmers used to maintain specific landraces on their farms, based on panicle and grain characters, growth duration, agronomic performance in local edapho-climatic conditions, as well as cultural uses (Rana et al 2007; Sajise et al. 2012). To continue cultivation of their favoured landraces, traditional farmers used to maintain the genetic purity of the landraces over centuries – just as today's dog breeders are careful to maintain pure breeds of Rottweiler and Dachshund by preventing cross breeding. An ancient method of maintaining genetic purity is to eliminate "off types" from the preferred landrace population (FAO 2016). One way to prevent cross pollination in cereals between cultivars grown on neighbouring plots is to de-synchronize the flowering of neighbouring landraces (Deb 2006) – a method which necessitates keeping a record of the respective flowering periods of different cultivars. Unfortunately, modern farmers, habituated to procuring breeders' seeds from the state and/or seed corporations, have forgotten this ancient art and science of "rouging" and the method of cross-pollination prevention. The UPOV and similar legal regimes in industrial countries disallow farmers to maintain a proprietary seed stock on-farm beyond a year. In the countries like India adopting certain sui generis system of legal protection of farmer rights (Lushington 2012), farm saving of seeds is protected. Nonetheless, a majority of farmers in South Asia rely on commercial seed supply, which obviates the need to conserve the purity of homegrown seeds (Deb 2019).

The loss of the genetic purity of landraces entails significant erosion of crop genetic diversity. With unrestrained gene exchange between different landraces, distinctive phenotypes of the different landraces disappear, implying reduction, and even obliteration, of the genetic distance between the crossed landraces. This eventually reduces the total number of landraces. In addition to the rapid replacement of folk crop landraces with modern HYVs, the loss of genetic purity of the extant landraces escalates the process of genetic erosion of the crop species. Unless the farmers and seed researchers take urgent measures to maintain the genetic purity of the vanishing landraces, further loss of the landraces and their distinctive genetic combinations that confer valuable characters (such as flood tolerance, salinity-tolerance and pest resistance) is likely inevitable.

## The second episode of taxic and genetic bottleneck of agrobiodiversity

The increment in diversity at ecosystem, taxic and genetic levels gained during the process of domestication over millennia and in the development of indigenous agroforestry systems was accompanied by the loss of some wild progenitors and in the loss of the original genetic diversity, which were lost in the artificial selection pressure. As discussed above, a significant proportion of the genes of the extinct progenitor species still survive in the domesticates; and the anthropogenic addition of new taxa as well as agroecosystems were new additions to the global repertoire of life forms. This gain, however small compared to the loss of species and ecosystems during the Pleistocene, began to eroded by the new phase of human civilisation a few centuries ago. The advent and the global spread of industrial development entailed rapid land use changes, leading to irreversible losses of habitats and biodiversity at an increasing tempo.

In addition to the forests and wetlands ecosystems, traditional biodiverse agroecosystems began to disappear with increasing urban-industrial growth and intensive agricultural landscapes. The introduction of intensive monocultures and the widespread application of industrial agrochemicals and machinery constituted a pulse perturbation to the complex traditional agroecosystems, severely truncating traditional crop species diversity and replacing complex agroecosystem complexity (in terms of crop and non-crop species combinations) with monocultures.. Pesticides and herbicides continue to eradicate a wide range of non-crop plants and animals, especially soil organisms and aboveground fauna from modern agroecosystems (Relyea??), radically truncating the on-farm food web complexity (Deb 2009b). Thus, the initial gain in biodiversity through domestication and agroforestry experiments over the past millennia is now being lost at an escalating pace.

Since the advent of global agricultural modernisation in the 1960s, drastic genetic erosion in all crops has been recorded on all continents; the loss of important phenotypic traits, alleles and gene combinations have pushed thousands of traditional landraces to extinction from farm fields (Ahuja & Jain 2015; Deb 2017; Nelson et al. 2019; Gadissa et al. 2021; Khouri et al. 2021; Ray 2022). India's largest folk rice gene bank, Vrihi (<https://cintdis.org/vrihi>) owns a live accession of 401 landraces collected from eastern India since 1996 (Deb 2005), of which 320 have disappeared from farm fields by the end of 2020 (Deb & Bhattacharya 2021), while new samples of extant aromatic landraces like Basmati, Gandheswari, Gobindabhog and Badshabhog rices of India are often aroma-less (unpublished acquisition records of Vrihi) – implying that the farmers growing these landraces no longer maintain the genetic purity of their heirloom rices. Over the last three decades, farmers have rapidly forgotten the science of characterisation and the art of "rouging" of off-types from their crop populations. As Gibson reported, the "perceptually distinctive" characters are seldom given importance in varietal selection criteria by contemporary generations of farmers, in participatory plant breeding programs and *in situ* conservation of plant genetic resources projects (Gibson 2009). The modern generation of farmers in South Asia frequently replace their traditional varieties with modern hybrid and high yielding varieties (HYVs) in expectation of higher yields (Rana??). Because the external supply of these modern seeds are easily available on market, farmers do not need to maintain the genetic purity of those seeds, which they replace every few year with a new batch of seeds. Thus, the ancient knowledge of genetic purity maintenance, based on perceptually distinctive characters, is lost. With the disappearance of this knowledge, most of the farmer landraces, which are not available on market, have lost their original characters for which they were selected and bred in the first place. Several commercial brands of Basmati rice marketed in South Asia and Jasmine rice in Thailand, for instance, are devoid of their characteristic aroma.

Genetic diversity erosion is also evident in domesticated animal breeds. According to a recent FAO estimation, "Cattle are the species with the largest number of breeds (159) reported as extinct. Large numbers of extinct breeds of sheep (107), horses (101), and pigs (70) are also reported. Some breeds may have become extinct without being ever documented." The total number of livestock breeds of domesticated mammals and birds that are classified as being at imminent risk of extinction is 2360, which is 27 percent of all breeds, including those that are extinct (FAO 2023).

## Misconceptions to be rectified

Regrettably, a good number of experts in modern agriculture and animal husbandry (especially in South Asia), in my personal experience, tend to ignore what Darwin recognised as the human "experiment on a gigantic scale" based on "initial variations", and tend to believe that the different indigenous breeds of cattle as well as rice are either wild or feral breeds. Many of the modern agriculturists and botanists are unaware of the pioneering contribution of E. K. Janaki Ammal, who traced the origins of a large number of domesticated plants to polyploidy, created by farmers' selection and hybridisation experiments with wild progenitor species (Darlington & Janaki Ammal 1945; Janaki Ammal 1951; Janaki Ammal & Gupta 1966). The root of this lack of awareness is in the high school and university curricula, oblivious of the custodian role of humans in conserving and expanding the biotic resource base. A proper biology curriculum ought to include the Darwinian and Vavilovian understanding of artificial selection and its determining influences on the course of human civilisation. Likewise, history curricula ought to include the history of domestication on different continents, that may create a general awareness about the ability of common people to nurture and expand local biological diversity.

A recognition of the process of domestication of plants and animals in the course of human civilization can reinstate the humankind's historic role as custodian and enhancer of biodiversity. This eco-constructive and custodian role is not an alternative to, nor compensatory of the eco-destructive role of humans, but is the other aspect of human social behaviour related to resource use. To describe the eco-destructive role of the human species as its evolutionary characteristic is scientifically wrong, and subscribes to a politically misleading worldview, engendering ineffectual policies to redress the environmental damages. A comprehensive description of human place in Nature in the Holocene must recognize the historical role of both the past and contemporary pre-industrial societies in enriching many ecosystems and even creating new taxa in the process of domestication, alongside the modern extractive economy that is detrimental of the natural world. This recognition would then exonerate humans as a *species* from the polemical blame of massive ecocides. It is important to acknowledge that the ecocidal crimes are committed only by a small section of humankind – a handful of industrial guilds and their cartel, directing the global techno-industrial economy and politics. A significant proportion of humankind, both in the past and current history, did not, and still do not, partake in any economic activities that may have any deleterious impact on biodiversity and the Earth's life support systems at a scale that a single industrial farmer or an opulent industrial-urban citizen does.

**Table 1.** The antiquity of domestication of an illustrative sample of domesticated animals and their progenitor species.

Species	Progenitor Species	Centre of Domestication	Approx. Domestication period (YBP)	References
Dog ( <i>Canis familiaris</i> L.)	Extinct common ancestor of <i>C. familiaris</i> and <i>C. lupus</i>	Near East	14,000	Galibert et al. (2011) Bergström et al. (2020)
Cow ( <i>Bos indicus</i> L.)	<i>Bos gaurus</i> Smith	Indus Valley	5,000	Fuller (2006)
Goat ( <i>Capra hircus</i> L.)	Bezoar ( <i>C. aegagrus</i> Erxleben)	Western Eurasia	11000	Driscoll et al. (2009)
Donkey ( <i>Equus asinus asinus</i> )	African wild ass ( <i>E. asinus africanus</i> )	Eastern Africa	4800	Driscoll et al. (2009)
Bactrian Camel ( <i>Camelus bactrianus</i> )	<i>Camelus bactrianus ferus</i>	Central Asia	5000-6000	Ji et al. (2009)
Horse ( <i>Equus caballus</i> )	Western Eurasian domesticate from <i>Equus ferus</i> (extinct)	Lower Volga-Don region	4200	Librado et al. (2021)
Llama ( <i>Lama glama</i> )	<i>Lama guanicoe</i>	Andean Valley	6000-7000	Fan et al. (2020)
Chicken ( <i>Gallus gallus domesticus</i> )	Red jungle fowl ( <i>Gallus gallus</i> )	East Asia, South Asia	4000 - 10000	Fan et al. (2020)
Silk moth ( <i>Bombyx mori</i> )	Extinct common ancestor of <i>B. mori</i> and <i>B. mandarina</i>	China	4100	Miao et al. (2013); Xiang et al. (2018)

**Table 2.** The antiquity of domestication and diversification of an illustrative sample of cultivated crops.

Species	Progenitor Species	Centre of Domestication	Domestication period (YBP)	References
Rice ( <i>Oryza sativa</i> ssp. <i>japonica</i> L.)	<i>Oryza rufipogon</i> Griff.	China	8,000	Choi et al. (2017)
Rice ( <i>Oryza sativa</i> ssp. <i>indica</i> L.)	<i>Oryza sativa</i> + <i>O. nivara</i> Sharma & Shastry	India	4,000	Choi et al. (2017)
Eincorn Wheat ( <i>Triticum monococcum</i> ssp. <i>monococcum</i> L.)	<i>T. monococcum</i> ssp. <i>aegilopoides</i> (Link) Thell.	Georgia	10,000	Faris (2014)
Common Bread Wheat ( <i>Triticum aestivum</i> ssp. <i>aestivum</i> L.)	<i>Aegilops tauschii</i> Coss.+ <i>T. turgidum</i> L.	Iraq	8,000	Faris (2014)
Emmer Wheat ( <i>Triticum turgidum</i> spp. <i>dicoccum</i> (Schrank) Schübl	<i>T. turgidum</i> ssp. <i>dicoccoides</i> (Körn.) Thell	Turkey	9,500	Faris (2014)
Corn ( <i>Zea mays</i> )	Teosinte ( <i>Zea mays</i> ssp. <i>parviglumis</i> Iltis & Doebley)	Mexico	8000	Piperno, (2011)
Barley ( <i>Hordeum vulgare</i> L.)	<i>Hordeum spontaneum</i> C. Koch.)	Israel-Jordan Tibet	12000	Badr et al. (2000) Dai et al. (2012)
Sorghum/ Guinea corn ( <i>Sorghum bicolor</i> )	<i>Sorghum arundinaceum</i> (Desv.) Stapf	Sudan	5500	Winchell et al. (2017)
Pearl millet ( <i>Pennisetum glaucum</i> )	<i>Pennisetum violaceum</i> (Lam.) Rich	Mali	4000	Fuller et al. (2021)
Quinoa ( <i>Chenopodium quinoa</i> Willd.)	<i>Chenopodium berlandieri</i> Moq.	Peru	6,000	Bazile et al. (2013)
Potato ( <i>Solanum tuberosum</i> L.)	<i>Solanum brevicaule</i> Bitter complex	Peruvian Andes	8000-10,000	Spooner et al. (2015)
Banana ( <i>Musa paradisiaca</i> L.)	<i>Musa acuminata</i> Colla	Melanesia	7000	Denham et al. (2003); Spooner et al. (2015)
Tea ( <i>Camellia sinensis sinensis</i> L.)	<i>Camelia</i> sp. (yet unidentified)	China	3000	Meegahakum-bura et al. (2018)



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