Biodiversity, Anthropogenic

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Abstract

A large number of Green discourses blames humans as a species for the current ecological crisis. However, this description serves to conceal the role of humans, in both past and contemporary pre-industrial societies, as custodians of biodiversity. Indigenous societies are known to conserve their natural resource base for posterity, by instituting cultural norms against exhaustive resource use. In addition, pre-industrial societies also increased biodiversity on species and genetic levels, by domestication of wild species. 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 species, 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 by of the new species created an abundance of distinctive crop landraces and animal breeds.

An unfortunate consequence of agricultural modernization is the erosion of on-farm genetic diversity of crop and livestock species worldwide. 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 humans in creating and conserving biodiversity will likely promote biodiversity conservation ethos in modern societies, and the value of genetic purity of the extant crop landraces.

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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 [1] 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 humakind. The continuing process of irreversible decimation of all wild habitats and biodiversity undoubtedly took an enormous scale and tempo over the past century, in all developed and developing countries, where all habitats are increasingly getting devoid of biodiversity. Ecosystem, species and genetic diversity of life are disappearing at an unprecedented pace, dwarfed only by that of the Cambrian mass extinction in geological past. 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 maintaining, and even enriching, biodiversity on Earth over millennia.

Humans as custodians of biodiversity

In contrast with the modern techno-urban-industrial *homo oeconomicus*, most of the human societies in the past millennia used to conserve their resource base for long term extraction and use, and enhanced species and genetic diversity, which still constitute the basis of production economies. Furthermore, there are millions of contemporary pre-modern societies who still remain largely ignorant or incapable of modern technology 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 and the Sentineli of the Andaman and Nicobar islands, the Yaaku and the Masai of Kenya have not pushed any species to extinction, despite the history of their hunting-gathering and fishing economies over millennia. Virtually all the past as well as contemporaneous pre-industrial societies have conserved biodiversity to sustain their respective resource base, by instituting cultural norms against exhaustive resource use [1]. Sacred species, sacred groves and seasonal restrictions on hunting and fishing are prominent examples of ancient cultural institutions of protection of the indigenous resource base. [1][2][3] A large number of endemic flora and fauna are still found in sacred groves and ponds in Asia and Africa.[4]

In addition to preserving the stock of bioresources for their own survival, and for future option value[4], indigenous societies have expanded the spectrum of biodiversity by adding novel species to the list of life forms on earth. Every domesticated species – plant or animal – is a new species that never existed before domestication. The domesticated biota were created by artificial selection and breeding of wild ancestral species over many generations. Darwin posited a revolutionary world view, explaining the origin of different species by means of 'selection' of variants among groups of organisms of common descent [5]. This process of natural selection was equivalent to the process of artificial selection by humans, for which he collated enough evidence in *The Variation of Animals and Plants Under Domestication*[6], four years before the last edition of *The Origin of Species*, [5] and noted the importance of the arduous process of anthropogenic creation of new species over thousands of years [ref. [6], 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 research in biodiversity and ecosystem structure.

Domestication of biota

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. [7] Later, beginning from the Neolithic, 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. [8] 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**.

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 (*Canis familiaris* L.)	*Canis lupus*	Near East	14,000	[9]
Cow (*Bos indicus* L.)	*Bos gaurus* Smith	Indus Valley	5,000	[10]
Goat (*Capra hircus* L.)	Bezoar (*C. aegagrus* Erxleben)	Western Eurasia	11000	[11]
Donkey (*Equus asinus asinus* L.)	*E. africanus* (**von Heuglin** & **Fitzinger**)	Eastern Africa	4800	[11]
Bactrian Camel (*Camelus bactrianus* L.)	*Camelus ferus* **Przewalski**	Central Asia	5000-6000	[12]
Horse (*Equus ferus caballus* L.)	*Equus ferus* L.	Lower Volga-Don region	4200	[13]
Llama (*Lama glama*)	***Lama guanicoe* (*Müller*)**	Andean Valley	6000-7000	[14]
Chicken (*Gallus gallus. domesticus* L.)	Red jungle fowl (*Gallus gallus* L.)	East Asia, South Asia	4000 - 10000	[15]
Silk moth (*Bombyx mori* L.)	*Bombyx mandarina* (Moore)	China	4100	[16]

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

Species	Progenitor Species	Centre of Domestication	Approx. Domestication period (YBP)	References
Rice (*Oryza sativa* ssp. *japonica* L.)	*Oryza rufipogon* Griff.	China	8,000	[17]
Rice (*Oryza sativa* ssp. *indica* L.)	*Oryza sativa* L. + *O. nivara* Sharma & Shastry	India	4,000	[17]
Eincorn Wheat (*Triticum monococcum* ssp. *monococcum* L.)	*T. monococcum* ssp. *aegilopoides* (Link) Thell.	Georgia	10,000	[18]
Common Bread Wheat (*Triticum aestivum* ssp. *aestivum* L.)	*Ae. tauschii* Coss.+ *T. turgidum* L. hybrid	Iraq	8,000	[18]
Emmer Wheat (*Triticum turgidum* spp. *dicoccum* (Schrank) Schübl	*T. turgidum* ssp. *dicoccoides* (Körn.) Thell	Turkey	9,500	[18]
Corn (*Zea mays*)	Teosinte (***Zea mays ssp. parviglumis Iltis & Doebley***)	Mexico	8000	[19]
Barley (*Hordeum vulgare* L.)	*Hordeum spontaneum* C. Koch.)	Israel-Jordan Tibet	12000	[20] [21]
Sorghum/ Guinea corn (*Sorghum bicolor*)	*Sorghum arundinaceum* (Desv.) Stapf	Sudan	5500	[22]
Pearl millet (*Pennisetum glaucum*)	*Pennisetum violaceum* (Lam.) Rich	Mali	4000	[23]
Quinoa (*Chenopodium quinoa* Willd.)	*Chenopodium berlandieri* Moq.	Peru	6,000	[24]
Potato (*Solanum tuberosum* L.)	*Solanum brevicaule* Bitter complex	Peruvian Andes	8000-10,000	[25]
Banana (*Musa paradisiaca* L.)	**Musa acuminata *Colla***	Melanesia	7000	[26]
Tea (*Camellia sinensis sinensis* L.)	*Camelia sp.* (yet unidentified)	China	3000	[27]

Criteria of animal domesticability

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 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 species 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. [28] During this transition, the animal population becomes accustomed to the human presence and a strong selection for docility in the animal shapes its behaviour. [29]

Selection and breeding of the selected progeny from the original progenitor stock is essential for creating a distinctively different domesticated species. Many breeds of domestic animals are incapable of living in the wild, and their recent wild ancestors are extinct. A case in point is the domestic silk worm, *Bombyx mori* [30]. The honey bee (*Apis mellifera*) is considered a domesticated insect, but in reality, has never been properly domesticated [31]. Instead, humans have learned to manage them for 7000 years —albeit in sophisticated ways—by providing them with artificial hives, and sometimes also providing them with unnatural sugar solution as a substitute for nectar, that make it easier to rob them of their honey and wax.

Larson and Fuller [32] surmise two alternative pathways of 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. After domestication, the animals are 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 iteroparity. This primary economic imperative of food security in every generation was the principal drive for domesticating an animal, which must either breed frequently or have a large litter size.
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). [33]
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 Piggott poignantly informs in his South American Idyll. [34]

   The courtship of the llama
   Embarrasses the farmer
   But it copulates far sooner
   Than the kinkier vicuña.
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,[35] and donkey (*E. africanus asinus*) were domesticated from the ancestral stock of *E. africanus,* [36] 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, [37] although Near Eastern gazelle hunters in the Epipaleolithic practiced a game management strategy to avoid culling reproductive females to promote persistence of the gazelle population. [38]

Conservation consequence of domestication

The fact that much of the genomes of several species now extinct are preserved in their domesticated progeny indicates that domestication has a conservation function. The extinct progenitor species of modern horse, cow, sweet potato and wheat are examples. 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*) [39] and the European honey bee (*Apis mellifera*)[31]. Aside from direct economic utility, cultural and religious values also encourage domestication, leading to conservation of several biota. The sacred basil (*Ocimum sanctum*), for instance, is ritually cultivated in millions of Hindu households in India, but is scarcely found in the forest [40].

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 by humans for consumption. [41] Successive breeders emphasised other important characters such as longer panicles (more edible grains), bolder and heavier grains (more starch) and basmati-like fragrance, imparted by 2-acetyl pyrroline (2AP). 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 saliva* 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. 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" [ref. [42], p. 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.

During the process of animal domestication, human-directed selection accounts for the initial appearance of traits that differentiated wild and domestic phenotypes. [32] The famous experimental study in animal domestication of Dimitry 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. [43] 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" [ref. [32], p. 117].

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. [44] 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. [42]. 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 [45][46]. 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 [21]. 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. [24] 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. [47] 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. [48][49][50] In addition to the direct economic value, gustatory and aesthetic preferences were also a driver of post-domestication selection of several morphological characters in crop landraces. [49]

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. [43] 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." [51]

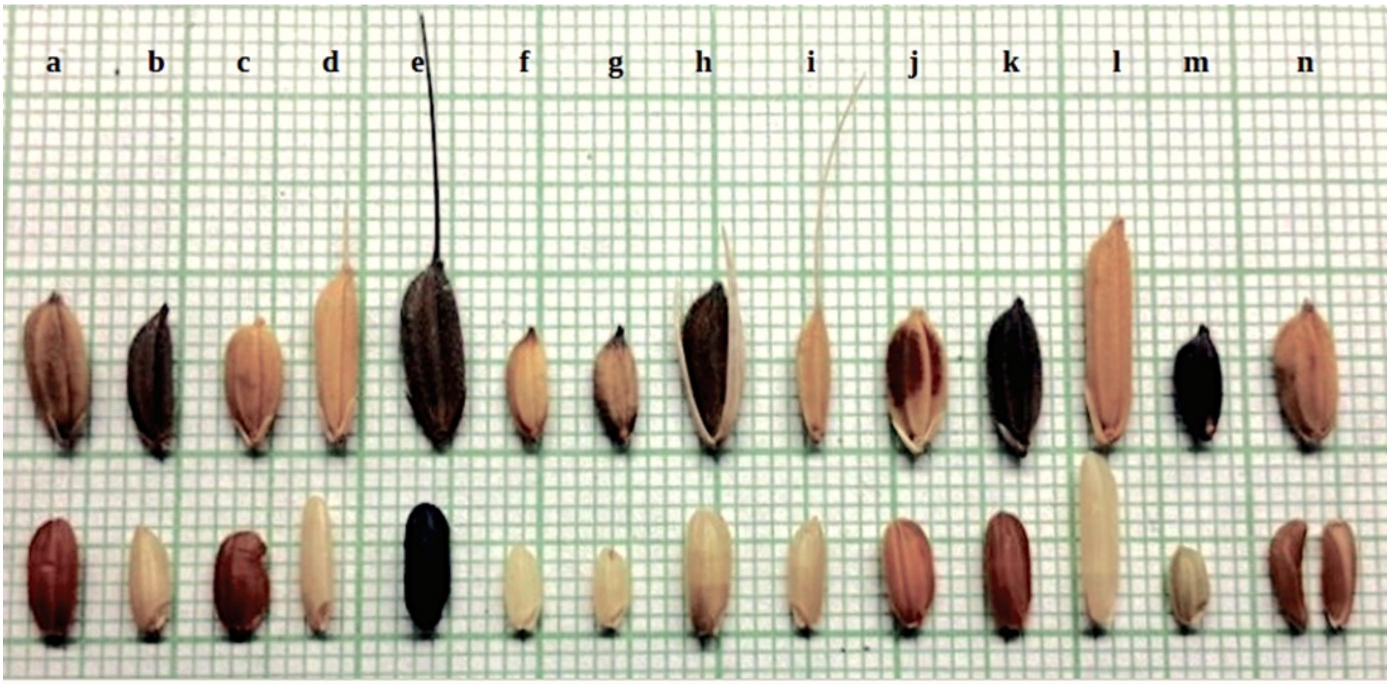

Fig. 1. A Glimpse of Rice (*Oryza sativa* ssp. *indica*) Genetic Diversity: showing rice grains (top row) with diverse awn size and colour (labelled **d**), (**e**), and (**i**); extra-long sterile lemma (**h**); and kernels (bottom row) with notched belly (**c**), black kernel (**e**) and double-kernel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

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. [47] The genetic bedrock of these traits, which constituted what Darwin called "the initial variation" inherent in the ancestral population were selected and amplified in pure lines of specific folk varieties. For instance, every pure line aromatic rice landrace is characterised by the homozygous inheritance of two recessive *BADH2* alleles (8 bp deletion in exon 7 and C/T SNP in exon 13) in each grain.[52]

An ancient method of maintaining genetic purity is to eliminate "off types" from the preferred landrace population. [53] Traditional farmers in fact maintained the genetic purity of their heirloom landraces over centuries - just as today's dog breeders are careful to maintain pure breeds. Another way to prevent cross pollination in cereals between cultivars grown on neighbouring plots is to de-synchronize the flowering of neighbouring landraces [54] – a method which necessitates keeping a record of the respective flowering periods of the 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 adopting certain legal protection of farmer rights, farmers have eventually become dependent on the commercial seed supply, which obviates the need to maintain the seed stock or genetic purity over years. As the traditional practice of seed assessment and rouging has disappeared among farmers, 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 in South Asia and Jasmine rice in Thailand, for instance, are devoid of their characteristic aroma.

Tasks ahead: Recognition and rectification

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. The root of this ignorance is in the high school and university curricula, which are generally silent about 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 wild plants and animals in the course of human civilization can reinstate the humankind’s historic role as custodian and enhancer of biodiversity. This recognition would also exonerate the human *species* from the polemical blame of massive ecocidal crimes, which are committed only by a handful of industrial guilds and their cartel, directing the global industrial economy and politics.

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