

Crop domestication in the Asia Pacific Region: A review



Pauline Okemo^{a,b}, Upendra Wijesundra^a, Upuli Nakandala^a, Natalie Dillon^c, Rahul Chandora^a, Bradley Campbell^a, Millicent Smith^a, Craig Hardner^a, Charles A. Cadorna^d, Guillaume Martin^{e,f}, Nabila Yahiaoui^{e,f}, Olivier Garsmeur^{e,f}, Nicolas Pompidor^{e,f}, Angeliqne D'Hont^{e,f}, Robert J. Henry^{a,b,*}

^a Queensland Alliance for Agriculture and Food Innovation, University of Queensland, Brisbane 4072, Australia

^b ARC Centre of Excellence for Plant Success in Nature and Agriculture, University of Queensland, Brisbane 2072, Australia

^c Department of Agriculture and Fisheries, Mareeba 4880, Australia

^d Institute of Biology, University of the Philippines, Diliman, Quezon City 1101, Philippines

^e CIRAD, UMR AGAP Institut, Montpellier F-34398, France

^f UMR AGAP Institut, Université Montpellier, CIRAD, INRAE, Institut Agro, Montpellier, France

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ABSTRACT

Understanding crop domestication provides a basis for ongoing genetic improvement of crops, especially in the utilization of wild crop relatives as a source of new variation and may guide the domestication of new crops. The Asia Pacific region is home to most of the world's human population and is a region in which many important crops were domesticated. Here we review the domestication of banana, citrus, coconut, macadamia, mango, millet, mungbean, rice, sugarcane and taro in the Asia Pacific region. These examples illustrate the importance of this region in the development of agriculture. The challenges of conservation of the genetic resources for these crops are exacerbated by the large human population and rapid economic development in the region. Advances in genetic technologies provide an opportunity for accelerated genetic improvement of these crops and the domestication of new crops.

1. Importance of crop domestication in the Asia Pacific region

The origins of agriculture have often been associated with the domestications in the fertile crescent in west Asia beginning more than 10,000 years ago. Modern perspective on the origins of agriculture recognize that the agriculture was initiated many times in diverse regions [1]. The domestication of tropical species has been studied in less detail but may have origins that date back to the same time. Early domestication of crops in the Asia Pacific region (Table 1) may have paralleled the early crop domestications in the fertile crescent of west Asia. The Asia Pacific region is home to many countries including China, Indonesia, India, Pakistan, Papua New Guinea, Fiji, Solomon Islands, Oceania region including Australia and New Zealand. The region centred on South-East Asia with warm, humid, tropical and sub-tropical climate is where many important tropical crop species originated. The Asia Pacific region (Fig. 1) is also home to a large proportion of the global human population (Fig. 2), and this is where most food is needed. Key species from this region include rice, possibly the world's most important food crop and

sugarcane, the crop harvested in the greatest quantities globally. Pulses domesticated in this region include soybean, azuki bean (4000–6000 years ago) [2] and mungbean. Other notable species include banana, citrus, taro, millet and mango. Macadamia is an example of a very recent domesticate (last 100 years). Here we review the available evidence on the domestication of these crops and their future potential. Domestication of tropical species has involved unique challenges. Tropical species are subject to intense biotic stress in tropical environments and may have limited tolerance to low temperatures preventing their cultivation in more temperate regions.

2. Climate change and the growing importance of tropical crops

Global warming is bringing more tropical environments to temperate regions allowing the spread of tropical crops and increasing the importance of these crops in global food production [3]. Cultivation of tropical crops has been affected by various elements of climate change. Due to their adaptation to warm and humid conditions, they

* Corresponding author. Queensland Alliance for Agriculture and Food Innovation, University of Queensland, Brisbane 4072, Australia.

E-mail address: robert.henry@uq.edu.au (R.J. Henry).

Table 1
Crop domestication in the Asia Pacific.

Crop	Site of Domestication	Time Since Domestication Years	Reference
Banana	SE Asia	7000	[76]
Citrus	SE Asia	2000	[84]
Macadamia	Australia/Hawaii	100+	[162]
Mango	India/SE Asia	4000	[110]
Millet	China/SE Asia/India	8000+	[47]
Mung bean	SE Asia	9000	[56]
Rice	Asia	7000	[7]
Sugarcane	New Guinea	8000	[132]

may be beneficial in diversification of crop species across the globe [4]. Some areas that were previously not suitable for tropical crop cultivation may become available due to changes in climatic patterns. These crops may provide important new options for crop production at higher latitudes [5]. Harnessing the benefits provided by these crops will be beneficial in advancing research and innovation in agriculture. However, climate change and expansion of human populations in the region threatens the survival of wild genetic resources for many key crops making it harder to understand the domestication process. Increased conservation utilization of the genetic resources of these crops is essential for food security.

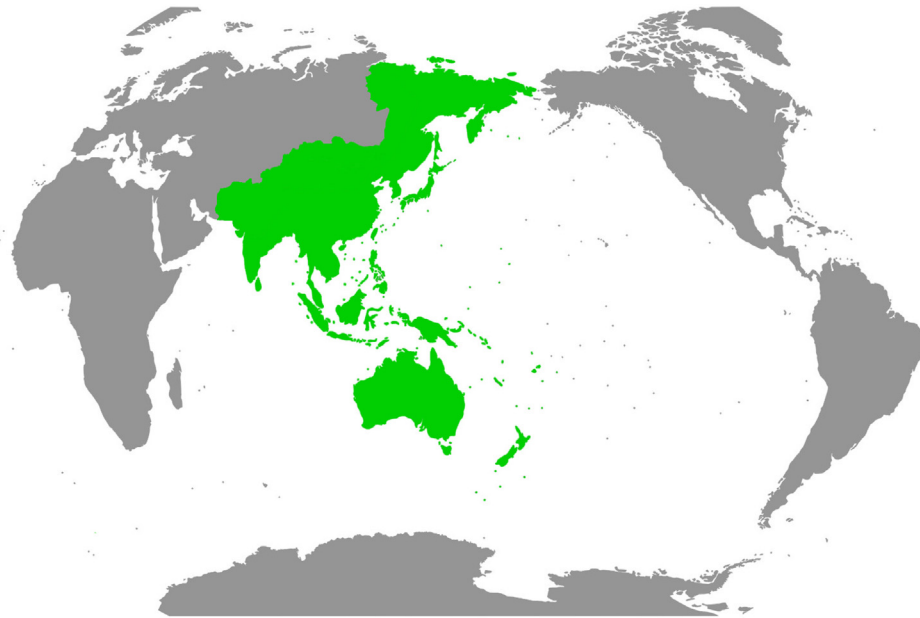


Fig. 1. World map. Green highlight representing Asia Pacific Region. The base map is based on the standard map with review number GS(2016)1561 downloaded from the website of China’s Ministry of Natural Resources standard map service.



Fig. 2. The Valenepieris circle. More people live inside this circle than outside NASA, Valerie Pieris, cmglee, CC BY-SA 4.0, via Wikimedia Commons.

3. Advances in understanding the domestication of crops in the Asia Pacific region

Agriculture relies on understanding the biology and genetics of plants to support crop management and continuing genetic improvement. Improved understanding of the domestication of these species reveals wild populations that need to be conserved as a resource for breeding and ways that this diversity might be accessed for crop improvement. Advances in genomic technologies [6] are facilitating more comprehensive analysis of the genomes of both domesticated and wild populations providing new evidence of domestication pathways.

4. Cereal domestication

Cereal crops are major sources of calories in human diets. The major cereal crops are wheat and barley domesticated in fertile crescent, maize domesticated in the America and rice domesticated in Asia and separately later in Africa. Sorghum was domesticated in Africa with most diversity in the genus being found in northern Australia and millet was domesticated in several locations including Asia.

4.1. Rice

The domestication of Asian rice has been the subject of much analysis with a range of evidence that has been interpreted as anything from a single [7] domestication event to two [8], three [9] or many. Sites of domestication in south China [10], South-East Asia [11] and India [9] have been proposed. Arguments for a single domestication have been based upon the presence of common domestication loci in the nuclear genome [10]. However, the distinct subspecies of *Oryza sativa*, indica and japonica, suggest the likelihood of separate domestications. This has been confirmed by the discovery that the domesticated gene pool contains only two functionally distinct chloroplast genotypes [8,12] despite the more complex diversity found in the nuclear genomes. The two chloroplast types do not currently correspond directly with japonica and indica nuclear genome types [8]. Two material domestications may have been followed by wide human distribution of the two types within Asia allowing extensive gene flow from local wild rice populations to deliver the diverse range of nuclear genome types found in the modern domesticated gene pool.

The primary gene pool for rice comprises the wild AA genome *Oryza* species (close relatives interfertile with domesticated rice [13]). These progenitors of domesticated rice are distributed across South and East Asia and Northern Australia [14]. The most divergent species in this group is *Oryza meridionalis* [15] found widely across Northern Australia. Another distinct taxa in Australia [16,17] is morphologically similar to *Oryza rufipogon* in Asia and is a sister to the clade that were the progenitors of domesticated rice in Asia [18,19]. The wild *Oryza rufipogon* and *Oryza nivara* populations in Asia may have contributed the two maternal (chloroplast) genomes found in the domesticated gene pool. They may have also contributed to the japonica and indica nuclear genome types that have recombined with the two maternal genome types in subsequent events.

The wild gene pool of rice is not well conserved either in situ [20] or ex situ [21]. Many wild rice populations are being lost to development before significant collections have been made [22]. The wild populations represent a key reservoir of gene diversity for use in rice improvement and more urgent efforts are needed to conserve this diversity in the wild and in seed banks.

De novo domestication of wild rice species has been proposed [23–25] and may be an important option for development of rice varieties for production in altered climates.

4.2. Millet

Millet is a heterogeneous group of small-grained, annual, hardy, warm-weather C4 cereals and are among the staple crops of semi-arid tropical regions of Asia and Africa [26].

Millet has been domesticated in almost every continent with prehistoric farming, except Europe [27–29]. Archaeological evidence suggests that millets, including Broomcorn millet/common millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*), were first domesticated about 8000–10,000 years ago in the Yellow River region of northern China [30–34], bridging the gap between nomadic hunter-gathering and organized agriculture [35,36]. The most important evidence for this early domestication, based on phytoliths and biomolecular pieces of evidence, is the identification of common millet from recently excavated grain storage pits at the Neolithic Cishan site, near the junction between Loess Plateau and the North China Plain, dated between ca. 10,300 and ca. 8700 calibrated years before present (cal yr BP) [30,37]. Subsequently, the recovery of ancient starch grain assemblages from stone tools excavated from the North China Plain also indicates the use of millets as early as 10 cal yr BP, while additionally suggesting an extended period of domestication of foxtail millet over two millennia [36,38]. By the late third millennium BC, millets had spread into Central Asia, Kazakhstan and south-westwards into South Asia [39,40]. *S. italica* (foxtail millet) is thought to have been domesticated from wild populations of *Setaria viridis*, around 8700 years ago, in northern China [38], while nuclear and chloroplast DNA sequences suggest that *P. miliaceum* (Proso millet), an allotetraploid species, has *Panicum capillare* as the maternal ancestor and the other genome being shared with *Protea repens* [31].

Closely related species of the same genus show independent domestications on different continents such as *Panicum* in China, India, and North America; *Echinochloa* in South Asia and Japan; *Setaria* in China, India, and Mesoamerica; *Digitaria* and *Brachiaria* in Africa and South Asia; *Echinochloa frumentacea*, derived from the wild progenitor *Echinochloa colona* (L.) (Jungle rice), showed a parallel line of evolution, both in India and Africa [39]. Japanese millet is believed to have been domesticated from wild populations of *Echinochloa crus-galli*, ‘barnyard grass’ in Japan, around 4000 years ago [41,42].

Panicum sumatrense (Little millet) is thought to have been domesticated in the Eastern Ghats region of India, where it forms a major portion of the diet of indigenous communities [43]. It is generally identified as tetraploid $2n = 4x = 36$ [44,45] although hexaploidy ($2n = 6x = 54$), has been reported [46] in the species. Little millet consists of the nana and robusta races, each of which comprises two subraces: laxa and erecta for nana, and laxa and compacta for robusta. *P. sumatrense* subsp. *psilopodium*, is a wild progenitor of Indian millet [43]. *Paspalum scrobiculatum* L. (Kodo millet) is estimated to have been domesticated around 3000 years ago, in the southern regions of Rajasthan and Maharashtra, located in western India [41], and widely cultivated in the Deccan Plateau region. *P. scrobiculatum* occurs wild across the Old-World tropics [42]. de Wet [47] described the classification of Kodo millet into the races regularis, irregularis, and variabilis. The domestication of *Brachiaria ramosa* (L.) occurred in the Deccan region of Southern India, around the beginning of the 3rd millennium BCE [48]. These three millets, little millet (*P. sumatrense*), kodo millet (*P. scrobiculatum*), and brown top millet (*B. ramosa*), are considered heritage crops of India, due to their historical significance, nutritional value, and cultural importance in the diverse cuisines of India. There is a lack of information regarding the geographic distribution and on-farm conservation of minor millets which poses a common challenge for their conservation and sustainable use faced by many neglected and underutilized species [49]. Several of the millets, cultivated in very localized areas or documented merely as archaeology, have been reported to be lost or disappearing [29].

Due to the domestication syndrome, many domesticated grain crops exhibit a variety of features, including reduced seed shattering, reduced seed dormancy, and free threshing [36,44,45]. The discrepancies have prompted a reconsideration of the optimal plant phenotype, known as the ideotype, in grain crops, suggesting that the domestication syndrome phenotype may be the most efficient ideotype in intricate agroecosystems [45]. The fixation of domestication syndrome has occurred over a considerable period and in a staggered manner [50,51]. To truly

comprehend the origins of domestication, it is crucial to understand how the domestication syndrome traits came to be [52].

5. Pulse domestication

Pulses are a key source of protein in human diets. Pulses have been domesticated in many parts of the world.

5.1. Mungbean

Mungbean (*Vigna radiata* (L.) Wilczek var. *radiata*) is a versatile food and cash crop that has been cultivated for thousands of years. The seed is consumed in a wide array of dishes including salads, stir-fry, noodles, dal and desserts, used as animal food and green manure and increasingly processed into plant protein products such as egg [53,54]. Mungbean production occurs across the tropics and sub-tropics with most production occurring in Southeast Asia including India, Pakistan, Bangladesh and expanding to other regions including East Africa and Australia [53,55].

The progenitor of domesticated mungbean *V. radiata* var. *sublobata* is likely of Indian origin [56] and recent studies using whole-genome sequencing have provided more insight and confirmation [57]. Domestication of mungbean occurred approximately 9000 years ago with loss of pod shattering and later improvement for determinate growth habit. Wild mungbean (var. *sublobata*) is also found in Australia with evidence of domestication traits noted, including reduced shattering and larger seed size [58]. Divergence from the Asian progenitor suggests introduction coincides with human movement into Australia ~50,000 years ago [57].

Today, mungbean is cultivated in many countries and production continues to expand due to its suitability in wide range of climates, value to agronomic production systems and nutritional versatility.

6. Domestication of root tubers and fruit crops

6.1. Banana

Various disciplines, including botanical observation, genetics, linguistics and archaeology have been used to understand the origins and domestication of the cultivated banana [59–64]. The main domestication trait of cultivated bananas is the edibility of their fruits which result from parthenocarpic development and bear no seeds. Such edible cultivars, selected by humans some thousand years ago, are since then vegetatively propagated. The pivotal role of the species *Musa acuminata* in cultivars origin has been known since early morphological observations [59,60]. Several *Musa acuminata* subspecies are geographically distributed in different regions along Southeast Asian regions and islands up to New Guinea [65] and some of them differ in their genome structure by large chromosomal rearrangements [66]. The subspecies *M. acuminata* ssp. *banksii* from New Guinea, *M. acuminata* ssp. *zebrina* from Java island and *M. acuminata* ssp. *malaccensis* from the Malayan peninsula and Sumatra island have for many years been identified as *M. acuminata* contributors to cultivar genomes while a fourth *M. acuminata* genetic group “*burmannica*” is less frequent in cultivars e.g. Refs. [60–62,67,68]. Results of multidisciplinary research were synthesized to infer a domestication process [63]. This model of domestication proposes that human travel or trade favoured hybridization between previously isolated *M. acuminata* subspecies in different contact zones from Southeast Asia up to New Guinea, leading to the production of edible diploids [63]. Unreduced gametes were produced by some of these diploids and further hybridizations within *M. acuminata* or with *Musa balbisiana* led to the majority of known triploid cultivars [63]. *Musa schizocarpa* from New Guinea or species from the *Australimusa* series were also identified in few cultivars [69–71]. The Fe'i (or Fehi) cultivars present in New Guinea and Polynesia area is the only group not deriving from *M. acuminata* but from species of the *Australimusa* series and represent a specific case, still to be precisely characterized, in banana domestication [72].

In parallel with this model, some diversity studies highlighted an important role of the *banksii* genetic group and notably found that a set of diploid cultivars (landraces) in Papua New Guinea are closely related to the local subspecies *M. acuminata* ssp. *banksii*, suggesting a particular domestication scheme there, independent of hybridisation [61,64].

Recently, the characterization of mosaics of genome ancestry along cultivar genomes revealed that cultivated bananas have complex ancestry patterns with three up to possibly 7 ancestors, including unknown ancestors [73,74]. However, the *Musa acuminata banksii* genetic group and a second species from New Guinea, *M. schizocarpa*, are found as core ancestral contributors to the global diversity of banana cultivars [74]. The *M. acuminata* ssp. *zebrina* is also prevalent in analysed cultivars. New Guinea diploid cultivars with the simplest ancestry mosaics and cultivars from other regions of the world show conserved *banksii*/*M. schizocarpa* introgression breakpoints, indicative of shared ancestry. This leads to a scenario where domestication was likely initiated with inter-specific hybridization between *banksii* and *M. schizocarpa* in the New Guinea region [74]. *M. acuminata* ssp. *zebrina* may also have played a role in the domestication process.

Diversification of the cultivated banana followed with the spread of early cultivars along Southeast Asia and further hybridisation with local species and subspecies. These include previously known contributors such as *M. acuminata* ssp. *malaccensis*; *M. acuminata* ssp. *zebrina*, *M. acuminata* ssp. *burmannica*, *M. balbisiana*, *Australimusa* sp. and recently identified contributors such as *Musa acuminata* ssp. *halabanensis*; *Musa acuminata* ssp. *sumatrana* and possibly *M. acuminata* ssp. *truncata* [74]. Among the contributing species and subspecies, some are poorly represented in international collections and at least one unknown ancestor remains to be characterized [73–76]. This highlights the need for further exploration, characterization and protection of wild banana diversity in the Southeast Asia/New Guinea region. Learning more about this diversity should help to refine the domestication scenario. In addition, much remains to be understood about the genetic bases of domestication i. e. the origins of parthenocarpy and absence of seeds in the fruits in diploids and the traits contributed by different banana ancestors.

6.2. Taro

Taro (*Colocasia esculenta*, *Araceae*) has a rich history as a root and leaf crop that was the most widely grown food worldwide prior to the Columbian exchange [77,78]. Its cultivation spans tropical to temperate regions including Africa, the Mediterranean, Asia, and Oceania, reflecting a wide diversity of forms such as edible starchy mother corms, stolons, and broad peltate blade leaves [79]. Although it's extensively cultivated, the total number of distinct *Colocasia* species remains contentious, with current estimates around 20 [78]. A long-standing theory posits that taro's origins lie in the region from Northeast India to Southeast Asia, where it is believed to have been domesticated [80, 81]. However, evolving insights into taro's genetic and geographic origins have led to continuous questioning of this theory [80].

Recent studies have focused on the chloroplast DNA diversity of cultivated and wild taros, and closely related wild taxa. These studies unveiled the polyphyletic nature of taro, pointing to three major clades: one spanning both cultivated and wild taros e.g., *Colocasia esculenta* var. *aquatilis* and *Colocasia esculenta* var. *esculenta*, another exclusive to cultivated taros e.g., *Colocasia esculenta* var. *antiquorum*, and a third limited to wild populations from Southeast Asia to Australia and Papua New Guinea, e.g., *C. esculenta* var. *aquatilis* and *Celtis formosana* [81]. Interestingly, the tropical and temperate clades of cultivated taro appear to trace their roots to Southeast Asia, contradicting the hypothesis of taro's primary domestication in Papua New Guinea, which emerged based on archaeological evidence of early cultivation in the region [80–82]. Despite these initial findings, more research is needed to establish the evolutionary history of taro conclusively and to pinpoint the precise geographical origins of its cultivars.

6.3. Citrus

Citrus originated in Southeast Asia and is a long-lived perennial fruit crop which is thought to have been domesticated about 2000 years ago [83,84]. The most recent analysis based on chloroplast genomes, nucleotide diversity and genetic distance has identified ten pure ancestral species with an absence of inter-specific admixtures. Three of them (*Citrus maxima*, *Citrus medica* and *Citrus reticulata*) are thought to have given rise to almost all other cultivated varieties through hybridization and natural mutations [84]. Hybridization is a major driving force in domestication of perennial trees such as citrus [85]. Admixture analysis based on diagnostic SNPs for each pure ancestral species has identified the parental alleles of interspecific hybrids. Accordingly, *C. maxima* (pummelo) alleles were found in most of the mandarins, and *C. reticulata* (mandarin) and *C. maxima* alleles were found in oranges, grapefruits, and sour oranges. Lemon has been identified as having a tri-hybrid origin involving mandarins, pummelo and citron. Australian round lime alleles were also detected in some Australian finger limes [84].

Cultivated citrus produced as a result of domestication have altered characteristics from wild species in relation to fruit quality, juiciness, seed number, peel colour, yield, taste, apomixis, and disease resistance [86–91]. Fruit acidity, levels of secondary metabolites and tolerance to stresses have been reduced during domestication while fruit taste, yield and asexual propagation have increased [83]. A plethora of studies have focused on genes involved in desirable traits which facilitates understanding the genetic basis of domestication. Reduced acidity in cultivated varieties is controlled by a few key genes such as CitPH1, CitPH5 and transcription factors such as PH3, PH4 [92], bHLH [93]. Wild citrus species are rich in anthocyanin pigments, however most of the domesticated citrus have lost their ability to produce high anthocyanin levels. Ruby1 and Ruby2 genes form a cluster which regulates anthocyanin expression in citrus where Ruby1 acts as an anthocyanin inducer while Ruby2 acts differently on wild and cultivated citrus [94]. In addition, a few transcriptional regulators, AN1 (bHLH), AN2 (MYB), AN11 (WD-repeat), PH3 (WRKY) and PH4 (MYB) are involved in anthocyanin regulation in citrus [95].

Juvenility is another important trait which has been targeted during domestication of citrus. Over the past few decades, efforts have been made to reduce the long juvenile phase of citrus trees by introducing early flowering genes. Inducing early flowering in apomictic seeds is a valuable approach to avoid graft-transmissible diseases in clonally propagated grafted trees and to expedite genetic improvement. Transgenic citrange overexpressed Arabidopsis APETALA1 (AP1) and LEAFY (LFY) genes have exhibited flowering in less than five years, compared to non-transgenic plants having a long juvenile phase (6–20 years) [96]. Polyembryony is also common in many cultivars except for a few including pummelo, clementine, citrons and some mandarin hybrids [97]. Apomictic cultivars have been preferentially selected during domestication to promote their clonal propagation [98]. Studies have been conducted to identify nucellar and zygotic plants through various genetic and morphology characterization approaches [99]. Polyembryony is thought to be induced by an insertion of an inverted repeat transposable element in the promoter of the CitRWP gene in polyembryonic citrus cultivars [88]. Moreover, seedlessness is also an important trait in citrus cultivars due to consumer preference. Cultivars with greater levels of parthenocarpy are preferred in this aspect and self-incompatibility and triploidy are two other means of obtaining seedless fruits in citrus [100,101].

Disease resistance is also a key factor in domestication. Australian wild limes including *Citrus australasica*, *Citrus glauca*, *Citrus australis*, *Citrus inodora* and close relatives including *Poncirus trifoliata*, *Murraya paniculata*, *Citrus latipes* have shown different degrees of resistance to HLB disease. In contrast, almost all the cultivated citrus are susceptible to this disease [102–104]. The resistance/tolerance is thought to be caused by genes encoding antimicrobial peptides [102], genes related to PR family, secondary metabolites, WRKY family, NBS-leucine-rich repeat proteins

(LRR) [105], and leucine-rich repeat receptor kinases (LRR-RKs) [106]. Similarly, almost all the cultivars are susceptible to canker disease while some wild species show resistance to canker disease. A primitive citrus species, *Atalantia buxifolia* is a canker resistant species due to the genetic variation of transcription factor gene TFIIA γ and the LOB1 gene promoter [107]. These examples illustrate the importance of wild citrus as sources of disease resistance for ongoing introgression into domesticated citrus. The production of high-quality chromosome level and haplotype resolved genome sequences for wild citrus [108] will facilitate their increased use in citrus breeding.

6.4. Mango

Cultivation of the common mango (*Mangifera indica*) dates back at least 4000 years [109]. According to historical reports, a single domestication event has been suggested [110] for mango and thought to be under cultivation in India for thousands of years prior to its introduction elsewhere [110]. However, the possibility of independent domestication events occurring in other areas apart from the center of origin has also been suggested [111]. It has been proposed that monoembryonic and polyembryonic mango varieties were domesticated separately in India and Southeast Asia, respectively [112–114]. Two gene pools identified between Indian and Southeast Asian mango populations [114,115] based on single nucleotide polymorphisms, further support the hypothesis of two centers of domestication. India has also recorded a few polyembryonic mangoes which are limited to the coastal region of the southwestern area [116]. But an analysis of Indian and Southeast Asian cultivars suggests the possible introduction of polyembryonic mangoes from Southeast Asia to India [114]. A recent population study suggested that mango domestication is more complex than previously understood and might include multiple domestication events and interspecific hybridizations [117]. Since crossbreeding between *M. indica* and wild relatives is evidenced within the genus [118–120], there is a probability of involving inter-specific hybridization during mango domestication. In contrast, *M. indica* shares similar geographical locations with its wild relatives due to domestication. This may have allowed inter-specific hybridization within the genus to occur.

In the initial phase of domestication, mango trees had small fruits with thin, acidic, and fibrous flesh that are still found in the regions of northeastern India. But the selection of superior seedlings over many centuries has resulted in fruits that have thicker flesh and large fruit size [116]. In the 4th and 5th centuries, Buddhist monks were thought to first introduce mangoes to Southeast Asia [110]. The introduction of mangoes to the western hemisphere of the world began when the trade between Asia and Europe started. During the 9th or 10th century, Persian traders spread mango to East Africa while the Portuguese reintroduced it from their territory in the 16th century [116]. The Portuguese further facilitated the mango distribution by introducing them to West Africa and Brazil from which it was spread throughout the Caribbean Islands. Mangoes were introduced to Mexico from both the Caribbean islands and the Philippines [119]. The first introduction to Florida was made in 1833 from Mexico followed by reintroduction in 1861–1862. Though the early introductions to Florida were not very productive, Mulgoba, which was introduced from India, was cultivated in a small scale. In 1910, the seedling selection of Mulgoba with fruits having an attractive red blush was named as ‘Haden’. During the 20th century, more mangoes were introduced from India and Southeast Asian countries to Florida. But microsatellite marker-based analysis has revealed that most of the Florida cultivars have derived from four Indian monoembryonic cultivars namely ‘Mulgoba’, ‘Sandersha’, ‘Amini’ and ‘Bombay’ with ‘Turpentine’ which has been introduced from West Indies [120]. Today, more than thousands of cultivars are under cultivation in India which are either landraces or cultivars originated by superior seedling selection. But many new commercially important cultivars in Florida such as Keitt, Kent, and Tommy Atkins have developed as a result of intensive breeding programs [121,122]. Due to

the diverse collection of mango germplasm developed in Florida, it is known as the secondary centre for mango diversity [122].

Apart from cultivated mango (*M. indica*), primary gene pool of genus *Mangifera* includes 68 other species and South-east Asia is the home for wild relatives [112]. The genus has originated in Indo-China, Burma, Thailand and Malay Peninsula representing centres of species formation [123,124] while Java, Sumatra, Borneo and Philippines have believed to be the secondary centre [111,125]. The majority of wild mango trees are found in tropical rainforests although a few species are widespread in swamp forests and in deciduous and semi-deciduous forests [126]. Other than *M. indica*, 26 mango species are known to produce edible fruits [127] and several wild relatives have potential traits useful in breeding including disease resistance (*Malosma laurina*) and abiotic stress tolerance (*Mangifera gedebe*, *Mangifera decandra*) [126]. Attempts of generating crossbreeds will be the first step towards developing improved cultivars with traits incorporated from wild relatives although very limited number of experiments have been carried out currently for inter-specific crosses [128].

Although wild species provide valuable genetic resource, many of them are classified under endangered species and lost in the wild even before they are discovered [126,129]. Several species have been classified as vulnerable (*Mangifera pajang*, *Mangifera zeylanica*, *Mangifera orophila*, *Mangifera similis*, *Mangifera flava* and *Mangifera macrocarpa*), data deficient (*Mangifera laljiwa*, and *Mangifera odorata*) and extinct in the wild (*Mangifera casturi* and *Mangifera rubropetala*) [130]. Information on the *Mangifera* gene pool were gathered and documented by several researchers [130] and importance in conservation efforts on *M. pajang*, *M. zeylanica*, *M. laljiwa*, and *M. odorata* have been documented [131]. But further actions must be planned and applied to conserve all the existing *Mangifera* species to be able to use them in future breeding programs.

6.5. Sugarcane

Sugarcane is an important industrial plant in subtropical and tropical regions, which provides around 80% of the world sugar production and is increasingly used to produce ethanol, as a substitute for fossil fuels. It is vegetatively propagated through stem cuttings. Sugarcane prehistory occurred in a vast area covering India to Polynesia. As for many tropical plants that are consumed for their vegetative organs, few remnants of sugarcane have been reported from archeological records [132]. Consequently, most theories on the domestication of sugarcane have been based on live wild and cultivated plants.

Sugarcane belongs to *Saccharum sensu stricto*, a genus composed exclusively of higher order polyploid (>4x) species. This genome complexity has complicated the reconstruction of phylogenetic relationships within the genus and other close genera. Several close genera (*Erianthus*, *Miscanthus*, *Narenga*, *Sclerostachya*) can occasionally hybridize with *Saccharum*. Based on morphological evidence, they have been proposed by some authors to be involved in the origin of *Saccharum* and are referred to as the 'Saccharum complex' by breeders (reviewed by Daniels and Roach). However, molecular data so far do not support an important direct contribution of these genera to *Saccharum* but suggest a monophyletic origin of this genus [133]. However, this does not exclude that natural intergeneric hybridizations could account for some local peculiarities.

The subdivision of the genus *Saccharum* is a matter of debate [134, 135], but a subdivision into six species is generally used by sugarcane technologists [133,136]. Among them, two species are wild (*Saccharum robustum* and *Saccharum spontaneum*) and four groups exist only in cultivation. These traditional cultivars have been described as species by botanists and have been given Latin binomials (*Saccharum officinarum*, *S. barberi*, *S. sinense* and *S. edule*) but should probably be considered as horticultural groups. The two wild species are well differentiated but for both the taxonomic limit and evolutionary history have been a matter of controversy (reviewed by Ref. [137]).

S. spontaneum is a highly polymorphic species that covers a huge geographic distribution from Africa to Southeast Asia. It generally has thin stalks with no or very low sugar content. It generally grows spontaneously in the vicinity of water resources. Its chromosome complement varies between $2n = 40$ and 128 [136] and distinct basic chromosome numbers exist with $x = 10$, $x = 9$ and $x = 8$, this last one being much more frequent [138,139]. The continental Asian origin of *S. spontaneum* is in little doubt because of the high morphological, cytological, and ecological diversity encountered there [136]. The general thinking is that *S. spontaneum* is not indigenous, east of Sulawesi although it can now be locally abundant [139]. It has been reported as an aggressive weed and sometimes behaves as an invasive species.

S. robustum has long thick stalks with little or no sugar. Typical habitat corresponds to mud banks along watercourses, but it is also encountered on humid slopes or along roadside ditches. Two cytotypes predominate with $2n = 60$ and $2n = 80$ with a basic chromosome number of $x = 10$ but chromosome number can reach up to 200 [140]. *S. robustum* has been reported as occurring in natural populations in the islands of Kalimantan, Sulawesi, Maluku, and New Guinea and in the Bismarck, Solomon, and Vanuatu archipelagos. The highest morphological diversity is clearly encountered in New Guinea [140,141]. Where it occurs in the wild, *S. robustum* is often planted in native gardens, either for medicinal purposes or as a material for building houses or fences.

The most popular scenario for sugarcane domestication, among sugarcane specialists, was first established by Ref. [141]. In this scenario, sugarcane originated in New Guinea from wild *S. robustum* by human selection possibly as much as 8000 years ago and resulted in a series of clones accumulating sugar in the stalks identified by botanists as *S. officinarum* ($2n = 80$). These cultivars were transported by humans to the Asian continent, where they hybridized with local forms of the wild species *S. spontaneum*, giving rise to a new series of cultivars better adapted to subtropical environments and to the emergence of sugar manufacturing [142]. They are called *S. barberi* for cultivars from India ($2n = 81-124$) and *S. sinense* for cultivars from China ($2n = 116-120$). The interspecific origin of these two groups of formerly cultivated sugarcane was demonstrated by molecular cytogenetics [143]. *S. edule* ($2n = 60-122$) is a peculiar small group of canes cultivated for their edible aborted inflorescence in subsistence gardens from New Guinea to Fiji. It is believed to correspond to natural mutant clones from *S. robustum* [133].

The origin of modern cultivars is well documented. They are all derived from a few interspecific hybridization events performed a century ago by breeders between the formerly cultivated groups *S. officinarum* and *S. barberi* and the wild *S. spontaneum*, followed by backcrossing with *S. officinarum* [136,144]. They have around 120 chromosomes with a majority of them inherited from *S. officinarum* and around 15–25 % from *S. spontaneum* including interspecific chromosome recombinants [139,145].

Genomic studies, so far, globally confirmed Brandes scenario. One notable recent exception is the study of Evans and Joshi (2016) [135], that suggested, based on chloroplast phylogenetic analysis, that two separated lineages diverged from *S. robustum* around 640K years ago. One of these lineages is proposed to have led to *S. officinarum* and the other to modern hybrid cultivars. They proposed giving this second lineage the status of a new species with *Sechium cultum* as its name. This hypothesis, however, is based on a very limited number of accessions and only on chloroplast sequence data and should be tested on the basis of a larger sample of accessions and nuclear sequence data.

Genomic studies often consider *S. officinarum* of autopolyploid origin [135,146]. However, Pompidor [146] recently analyzed all 12 hom(oe)ologous haplotypes sequences (BAC clones) from two distinct genomic regions of a typical modern cultivar, as well as the corresponding sequence in *Miscanthus sinense* and *Sorghum bicolor* and monitored their distribution among representatives of the *Saccharum* genus. The diversity observed among haplotypes suggested the existence of three founding genomes (A, B, C) in modern cultivars, which diverged between

0.8 and 1.3 Mya. Two genomes (A, B) were contributed by *S. officinarum*, and one genome (C) was contributed by *S. spontaneum*. These results suggested the presence of two founding genomes in *S. officinarum*, which were also found in its wild presumed ancestor *S. robustum*. This evolutionary model is still compatible with Brandes [141] scenario but represents a revision of the understanding of *Saccharum* diversity. This model is based on the analysis of two large genomic regions and would need to be re-assessed at the whole genome scale.

6.6. Coconut

Due to the absence of universal domestication traits in *Cocos nucifera* (coconut) and coupled with years of human interaction with this species, it has been hard to uncover the origin of coconut cultivation. However, molecular marker analyses (Restriction Fragment Length Polymorphism (RFLP), Simple Sequence Repeats (SSR), and Amplified Fragment Length Polymorphism (AFLP)) have suggested two genetically distinct groups [147–150]. These groups correspond to the Pacific Ocean and Indo-Atlantic Ocean basins, respectively. This was also supported by an extensive genetic analysis of coconut accessions found in different regions around the world. Analysis of several microsatellite markers from these accessions revealed two separate origins of coconut domestication in the Pacific and Indian Ocean basins [151].

Several coconut genome assemblies have already been published. These genomic resources provide insights on important biological traits such as salt tolerance, fibre content, and plant height [152,153]. It has been hypothesized that dwarf coconut varieties did not originate from tall varieties because genome sizes, as determined by flow cytometry, between these two cultivars were not different statistically [154]. However, SSR marker analysis revealed that dwarf coconut varieties originated from tall varieties in a single domestication event [155]. This result was also supported by whole genome sequence data comparison between “Hainan Tall” and “Catigan Green Dwarf” since there is a huge difference on genome sizes as indicated by k-mer analysis [156]. In addition, multi-omics analysis of tall and dwarf coconut varieties showed that human-driven breeding behaviour have led to the selection of dwarf coconut. Furthermore, there are differences in the expression of gibberellin (GA) biosynthetic enzymes GA-20 oxidase (GA20ox) and GA content between dwarf and tall coconut cultivars. Also, genome-wide association studies (GWAS) showed that GA20ox gene on Chr12 has affected height characteristics of coconut [153]. The ortholog of GA20ox gene is also responsible for plant height in other cultivated crops such as rice and wheat which led to the Green Revolution [157,158]. Moreover, this implies that the process of selecting for plant height consistently favored the preservation and propagation of a specific gene over millions of years. Given enough evidence, it is now clear that dwarf coconut cultivar has originated from tall variety due to domestication events.

6.7. Macadamia

The plant *Macadamia F. Muell* is one of the many rainforest genera of the ancient Gondwanic family Proteaceae [159]. As such, the genus lies within Basal Eudicots, in contrast to most of the common horticultural tree crops from the northern hemisphere [160]. Macadamia is native to the subtropical rainforest of eastern Australia [161]. Two of the species of macadamia (*Macadamia integrifolia* Maiden & Betche and *Macadamia tetraphylla* L.A.S. Johnson) produce highly valued kernels which have the highest oil content of common nuts (72%) [161]. Macadamia is the first plant from the flora of Australia to have been developed as an international crop following colonisation in the mid-1800s and, hence, is an example of recent rapid domestication [162].

Evidence of first nations utilisation prior to colonisation includes local indigenous names for the plant, implements designed for cracking the hard shell of the nut, and inclusion of the plant in oral history [161]. In addition, there may be evidence of translocation by first nations peoples

as the chlorotype of a few accessions sampled from apparently natural populations do not match the otherwise strong geographic structure of chloroplast variation [163]. Macadamia nuts were traded with settlers but, like most native foods of indigenous people, did not become a staple of the colonisers diet [164]. The first European planted macadamia appears to be a tree in the Brisbane Botanical Gardens; still alive from 1858 [161].

Although small scale orchards were planted in Australia in the late 1800s with germplasm collected from nearby native forest, the first commercial scale seedling orchards were planted in Hawai'i from the 1920s. These plantings were based on seed introduced from the 1800s, initially as a horticultural curiosity [165]. Following development of vegetative propagation, these seedling orchards were surveyed by the University of Hawaii to identify phenotypically elite individuals that were then clonally tested to identify 12 named cultivars (and additional selections) for release. Almost all Hawaiian cultivars and selections trace back to a single population at the north of the natural distribution of the main edible species *Macadamia integrifolia* [162], although one Hawaiian selection (791) is a tri-species hybrid [166]. Independent cultivar development was undertaken in Australia from the 1940s with material selected from nearby forests or garden plantings, and subsequently by combining these with Hawaiian cultivars [161]. Early South African cultivars were also developed from seed introduced in the late 19th century, but genetic improvement programs in most other countries are derived from improved Hawaiian and Australian germplasm.

The world industry has grown over the last 50 years; however, Hawaiian cultivars still dominate world production [165]. Macadamia cultivars are only 2–5 generations from the wild but have undergone rapid adaptation to commercial production [162]. There are opportunities for further development through ongoing selective breeding to increase productivity and reduce length of juvenility and tree size [167]. Development of disease and pest resistance requires well developed protocols for assessing these traits. While breeding may be able to influence kernel quality, there may be little market return for changes in these traits. Hybridisation of the edible germplasm with other smaller inedible species (*Macadamia janseni* C.L. Gross & P.H. Weston and *Macadamia ternifolia* F. Muell) is possible [161] and may offer opportunities for additional step change in tree architecture and other undiscovered characteristics [167]. Nevertheless, there is limited coordinated efforts to conserve the domesticated germplasm, and while several ex-situ collections of wild germplasm were made in the late 1900s, much of the native habitat of this genera has been cleared for agricultural development or are isolated remnant populations on private land [168].

7. Future crops: Conservation, genetic improvement and new domesticates

Domestication of many important tropical crops can be traced to South-East Asia. Areas to the south in Australia seem to have been the source of fewer domesticates despite the presence of unique biodiversity and many crop wild relatives [169]. This suggests the need for serious efforts to document the origins of agriculture in the Asia–Pacific region. This also makes the Asia–Pacific region a rich source of potential new domesticates especially in response to the requirements to adapt agriculture to climate change. Genomic analysis is accelerating the evaluation of genetic resources in Asia–Pacific and this should uncover further genetic resources that might find a role in agriculture and food production. Furthermore, genome editing is now being applied to domestication of new species from the Asia–Pacific regions. These could become important new crops. Tropical species from the Asia–Pacific regions are generally less well conserved in ex situ collections than more temperate species. Many important tropical species are also not effectively conserved in situ. The importance of these plants populations for global food security indicates the need for greater efforts to ensure conservation of genetic resources for plant species in these regions.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions

PO: Writing, review, and editing. UW, UN, ND, RC, BC, MS, CH, CC, GM, NY, OG, NP, and AH: writing and review. RH: Conceptualization, writing, review, and editing.

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