TRACING THE DOMESTICATION HISTORY OF MANGOSTEEN (*Garcinia mangostana* L.) USING MORPHOLOGICAL AND GENETIC APPROACHES

By

YAO TZE LEONG

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia and University of Montpellier in Fulfilment of the Requirements for the Degree of Doctor of Philosophy

November 2023

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Abstract of thesis presented to the Senate of Universiti Putra Malaysia and University of Montpellier, in fulfilment of the requirement for the degree of Doctor of Philosophy

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November 2023

Chairperson : Associate Professor Mohd Nazre Saleh, PhD
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Rainforests in Southeast Asia harbour a great diversity of edible fruits. One of the most emblematic is mangosteen (*Garcinia mangostana* L. var. *mangostana*; Clusiaceae), popularly known as the queen of fruits for its exquisite sweet-sour taste and aesthetic appearance. Previous cytological and phylogenetics studies reported contrasting results on the biological origin of the cultivated mangosteen. The more recent findings suggested the wild populations of *G. mangostana* var. *malaccensis* as the most probable sole progenitor of the cultivated mangosteen but the overview of its domestication history is far from complete. Against the backdrop of the contradictory theories of its biological origin, the current study set to trace back the domestication history of cultivated mangosteen. Our textual review revealed the earliest written records available indicated that fruits of mangosteen have been sold in marketplaces in the major seaports in the Malay Archipelago for at least 600 years. To elucidate the phenotypic affinities among the cultivated mangosteen and wild relatives, we used morphology as a proxy. In the morphometric analyses, we included 124 specimens consisting of cultivated and wild mangosteens. A total of 38 characters are included in this study. We used Principal Coordinates Analysis (PCoA) and Ascendent Hierarchical Classification (AHC) to evaluate the morphological characters used in species delimitation. Our findings showed that wild mangosteen species can be clearly delineated from cultivated mangosteen using morphological characters. However, we could not find character or combination of characters with statistical support that delimitate taxonomic varieties in *G. mangostana*. We employed cpDNA SNPs as the genetic markers to examine phylogeny and to infer haplotypes. We selected 192 individuals for genomic library construction. Raw reads were generated applying high-throughput shotgun sequencing. We plotted cladogram and haplotype network diagram to illustrate the genealogy of cultivated and wild mangosteen. The haplotype network consists of populations distributed in East and West Coasts of Peninsular Malaysia, Singapore, Sarawak, Sabah and Africa. This network enables us to interpret the effects of seed dispersals on geneflows in the cultivated and wild populations, a congregate haplotype consists of cultivated mangosteen from a few

regions exemplified that cultivated mangosteen is assumably disseminated by cultivators over long time. Among wild populations of var. *borneensis* and var. *malaccensis*, the geneflow is relatively localised. The localised geneflow is most probably the consequences of dispersals by primates. Considering the findings from morphometric and genetic analyses, we conclude that a distinction between the wild and cultivated compartments of mangosteen is not attainable. Regarding the domestication history, our findings demonstrated that the cultivated var. *mangostana* of Peninsular Malaysia and Singapore arose from the wild populations of var. *malaccensis*. We hope this study would spur interest among researchers across the Southeast Asian countries to further clarify the taxonomy, phylogeny and genetic diversities of wild *Garcinia* congeners, as well as other poorly understood cultivated trees at regional scope.

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Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia dan Universiti Montpellier, sebagai memenuhi keperluan untuk ijazah Doktor Falsafah

MENJEJAKI SEJARAH DOMESTIKASI MANGGIS (*Garcinia mangostana* L.) MENGGUNAKAN PENDEKATAN MORFOLOGI DAN GENETIK

Oleh

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Pengerusi : Profesor Madya Mohd Nazre Saleh, PhD
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Hutan hujan di Asia Tenggara kaya dengan kepelbagaian spesis pokok buah. Salah satu spesis yang paling terkenal ialah manggis (*Garcinia mangostana* L. var. *mangostana*; Clusiaceae), juga dikenali sebagai ratu buah-buahan kerana rasa manis-masam yang enak dan penampilan yang estetik. Kajian sitologi dan filogenetik sebelum ini melaporkan keputusan yang berbeza mengenai asal biologi manggis yang ditanam. Penemuan yang lebih terkini mencadangkan populasi liar *G. mangostana* var. *malaccensis* sebagai moyang yang paling berkemungkinan bagi manggis tetapi gambaran keseluruhan sejarah domestikasi masih jauh dari lengkap. Berlatarbelakangkan teori-teori yang bercanggah tentang asal usul biologinya, kajian ini bertujuan untuk menjejak sejarah domestikasi manggis. Kajian tekstual kami mendapati rekod bertulis terawal menunjukkan bahawa buah manggis telah dijual di pasaran di pelabuhan utama di sekitar Kepulauan Melayu selama 600 tahun sekurang-kurangnya. Untuk memperjelaskan pertalian fenotip antara manggis dan saudara liar, kami menggunakan morfologi sebagai proksi. Dalam analisis morfometrik, kami melibatkan 124 spesimen yang terdiri daripada manggis kampung dan taksa liar. Sebanyak 38 karakter morfologi diambil kira dalam kajian ini. Kami menggunakan *Principal Coordinate Analysis* (PCoA) dan *Ascending Hierarchical Classification* (AHC) untuk menilai karakter morfologi yang digunakan dalam persempadanan semula spesies. Penemuan kami menunjukkan bahawa spesies manggis liar boleh ditakrifkan dengan jelas berbeza daripada manggis menggunakan karakter morfologi. Walau bagaimanapun, kami tidak menemui karakter atau gabungan karakter dengan sokongan statistik yang membatasi jenis variasi taksonomi dalam *G. mangostana*. Kami menggunakan SNP cpDNA sebagai penanda genetik untuk kajian filogeni dan haplotip. Kami memilih 192 individu untuk *genomic library construction*. Bacaan jujukan dijana menggunakan teknologi *high-throughput shotgun sequencing*. Kami memplot rajah rangkaian kladogram dan haplotaip untuk menggambarkan silsilah manggis dan spesis liar. Rangkaian haplotaip terdiri daripada populasi yang bertaburan di Pantai Timur dan Barat Semenanjung Malaysia, Singapura, Sarawak, Sabah dan Afrika. Rangkaian ini membolehkan kami mentafsir kesan penyebaran benih pada aliran gen dalam populasi

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yang ditanam dan liar, haplotaip berkumpulan terdiri daripada manggis yang ditanam dari beberapa kawasan yang menunjukkan bahawa manggis yang ditanam mungkin disebarkan oleh penanam dalam jangka masa yang lama. Antara populasi liar var. *borneensis* dan var. *malaccensis*, aliran gen agak setempat. Aliran gen setempat kemungkinan besar adalah akibat daripada penyebaran oleh haiwan primata. Memandangkan dapatan daripada analisis morfometrik dan genetik, kami menyimpulkan bahawa perbezaan antara manggis liar dan ditanam tidak dapat dicapai. Mengenai sejarah domestikasi, penemuan kami menunjukkan bahawa var. *mangostana* Semenanjung Malaysia dan Singapura muncul daripada populasi liar var. *malaccensis* setempat. Kami berharap kajian ini menyemarakkan minat di kalangan penyelidik di seluruh negara Asia Tenggara untuk memperdalamkan kajian taksonomi, filogeni dan kepelbagaian genetik spesis *Garcinia* liar, serta spesis pokok-pokok buah lain yang kurang difahami pada skop serantau.

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Date: 14 March 2024

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LIST OF ABBREVIATIONS

AFLP	Amplified fragment length polymorphism
AHC	Ascendent hierarchical classification
BCE	Before common era
CE	Common era
CH index	Calinski–Harabasz index
cpDNA	Chloroplast DNA
DNA	Deoxyribonucleic acid
DYNADIV	Plant Biodiversity and Adaptation Research Group
FAO	Food and Agriculture Organization
FCM	Flow cytometry
I.F.A.C.	*Institut des fruits et agrumes coloniaux*
IRD	French National Research Institute for Sustainable Development
ISSR	Inter simple sequence repeats
ITS	Internal transcribed spacer
LGM	Last Glacial Maximum
MATAB	Mixed alkyltrimethylammonium bromide
nrDNA	Nuclear DNA
PCoA	Principal coordinates analysis
Pen. M'sia	Peninsular Malaysia
RAF	Randomly amplified DNA fingerprinting
RAPD	Random amplified polymorphic DNA
SEA	Southeast Asia
SNPs	Single nucleotide polymorphisms
SSRs	Simple sequence repeats
WGS	Whole genome sequencing
WMO	World Meteorological Organization

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction to cultivated mangosteen and its wild relatives

1.1.1 The cultivated mangosteen

Mangosteen (*Garcinia mangostana*, Clusiaceae) stands as an emblematic tropical fruit indigenous to Southeast Asia, renowned for its consumption in its fresh state and widespread popularity among the local population. Distinguished by its exquisite taste and aesthetically pleasing appearance, mangosteen has earned the epithet “queen of fruits”. Globally, mangosteen holds significance as a key export within the commodity cluster “Mango, mangosteen and guava” (FAO, 2020). While it has been introduced throughout the humid tropics, Southeast Asia remains the major production region for mangosteen (Osman & Milan, 2006). Presently, cultivation of mangosteen has expanded to encompass the American and African tropics as well (Lim, 2012; Murthy et al., 2018).

Osman & Milan (2006) have presented a comprehensive account on the husbandry of mangosteen. Cultivated mangosteen trees in orchards, featuring well-spaced planting distances, develop a roundish crown with dense foliage (**Figure 1.1**). Exudates from wounded sapwood appear as a mustard yellow and sticky substance (**Figure 1.2A**). The twigs and leaves of the mangosteen exhibit an opposite arrangement (**Figure 1.2B**), while the flowers emerge singly from the apical end of twigs (**Figure 1.2C**).

Figure 1.1 : Cultivated mangosteen trees in Taman Pertanian Universiti Ladang Puchong, Universiti Putra Malaysia planted at 12 by 12 m distance. The trees are 6–8 m tall and the tree trunks measured 30–40 cm diameter at breast height

The mangosteen fruit exhibits an oblate-globular shape with a measured diameter ranging 4–7 cm (**Figure 1.3**). The outermost layer of the mangosteen, commonly referred to as the rind, is thick and softly ligneous. The colour of the outer surface of the rind changes through ripening process, transitioning from white to pink, mauve and eventually to purple-black. Encased within the rind are the edible flesh, organised into four to eight unequal segments. Notably, the count of flesh segments aligns consistently with the lobes of persistent stigma plate. The glistening white flesh is both delicate and juicy, offering a mild sweetness with a subtle sourish tinge. Within the fruit, one might encounter one to three seeds in the larger flesh segments, while the smaller segments are typically seedless. It is noteworthy that completely seedless fruits are not a common occurrence.

Mangosteen has garnered substantial attention within the realm of research, mainly owing to its medicinal properties and unusual breeding system. While recent reviews of the previous have explored the medicinal aspects studies regarding the medicinal properties of mangosteen (Ovalle-Magallanes et al., 2017) and the origin of cultivated mangosteen (Yao et al., 2023), a critical gap remains in the understanding of its domestication history. Consequently, the present study aims to address this research gap by delving into the domestication history of cultivated mangosteen, employing population genetic studies that encompass both cultivated and wild varieties. To complement the population genetic approach, morphometric analyses have been incorporated, providing additional supporting information to augment the comprehensive exploration of mangosteen's domestication history.

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Figure 1.2 : The salient characters of mangosteen. A. sticky, mustard yellow droplets of exudates observed on the wounded sapwood; B. oppositely arranged twigs and leaves; C. an overmature flower without petals exposing the adaxial surface of sepals in red, ovary and stigma are white and numerous staminodes encircle the ovary base

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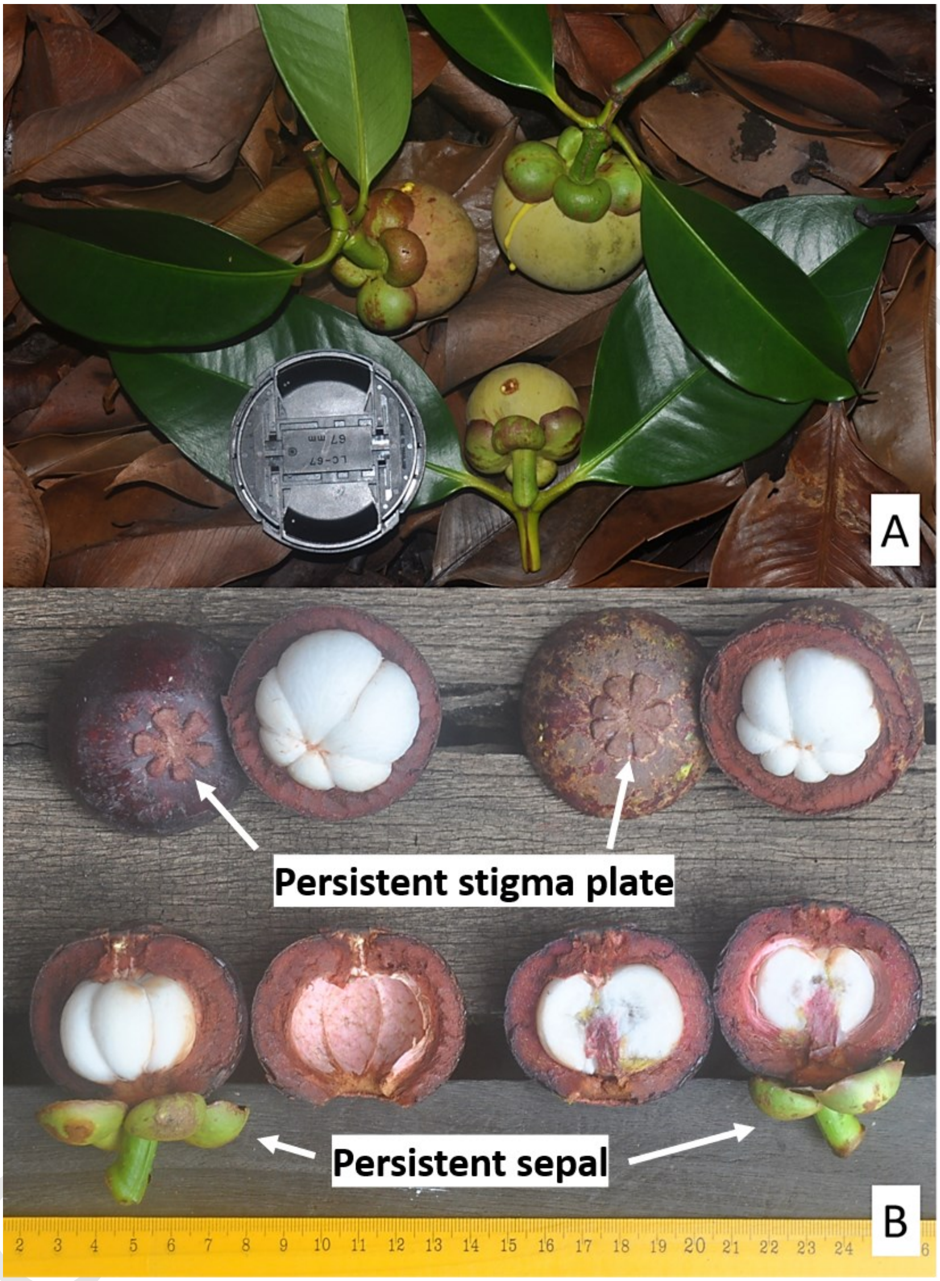

Figure 1.3 : The fruits of mangosteen. A. fruits issued from the apical ends of the twigs, young fruits are pale yellowish green; B. mature fruits with the rinds cut longitudinally (two fruits above) and vertically (two fruits below), pried apart to expose the flesh segments. Note that the number of flesh segments and lobes of persistent stigma plate are always count the same

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1.1.2 The wild varieties

Within taxonomic classification, mangosteen is the type species of *Garcinia* L. sect. *Garcinia*. This taxonomic section has undergone a recent revision, resulting in its circumscription to encompass a total of 13 species (Nazre et al., 2018). Notably, *G. mangostana*, the focus of this study, exhibits two taxonomic varieties within its natural habitat, namely (i) *G. mangostana* var. *borneensis* and (ii) var. *malaccensis*. In a phylogenetic analysis conducted by Nazre (2014), *G. mangostana* var. *mangostana* and var. *malaccensis* collectively form a paraphyletic clade, with var. *borneensis* emerging as the sister taxon to this paraphyletic clade. Key characteristics of the *G. mangostana* varieties are succinitly summarised in **Table 1.1**.

Table 1.1 : Main features of *G. mangostana* varieties

Taxon	Presence of pistillodes in male flowers	Fruit shape	Fruit size (across the widest dimension)	Fruit apex; persistent stigma plate shape, and surface texture	Cultivated or wild	Natural geographical distribution
mangostana	present*, c. 5 mm long	ovoid or globose	4–7 cm	rounded; circle, and smooth	cultivated; feral populations might exist	Malaysia and Indonesia
malaccensis	absent, or if present c. 2 mm	globose, ellipsoid or ovoid	3–4 cm	acute to attenuate; circle, and rugose	cultivated and wild; cultivated populations are called *mesta* in Peninsular Malaysia	Sumatra; Malay Peninsula; Borneo: Southwest Sarawak and Brunei
borneensis	absent, or if present c. 2 mm	globose	3–4 cm	rounded; circle or oval, and smooth to slightly rugose	wild	Borneo: East coasts of Sabah and Kalimantan

*Hambali and Natawijaya (2016) mentioned that the male flowers of var. *mangostana* described by Idris & Rukayah (1987) fell within the morphological plasticity of male flowers they observed in Sumatran *G. mangostana* var. *malaccensis* populations. (Adapted from Nazre et al. (2018))

The distribution of *Garcinia mangostana* var. *borneensis* encompasses the region of east Borneo, wheareas var. *malaccensis* is found in Sumatra, Peninsular Malaysia, and west Borneo (**Figure 1.4**). Notably, these taxonomic varieties serve as the primary candidates for the wild progenitors of the cultivated mangosteens.

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The vernacular names "*manggis*" and "*manggis kampung*" are commonly attributed to *G. mangostana* var. *mangostana* in Peninsular Malaysia. The wild var. *borneensis* occurs within the ecological research plots in natural forests in Kabili-Sepilok Forest Reserve, Sabah, Malaysia is referred to as "*manggis*". Meanwhile, the wild *G. mangostana* var. *malaccensis* is denoted as "*manggis hutan*" and known as "*mesta*" for the cultivated populations in Peninsular Malaysia.

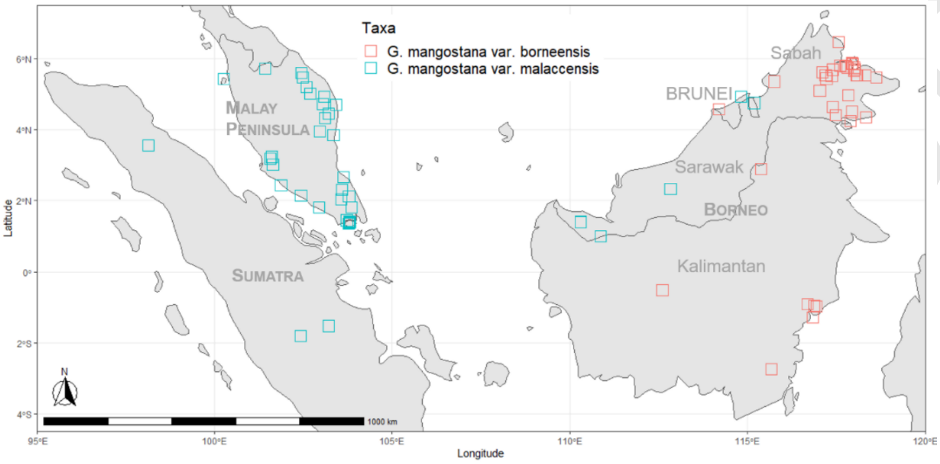

Figure 1.4 : Geographical distribution of *G. mangostana* wild varieties: var. *borneensis* and var. *malaccensis*

In West Java, distinct local names are employed to designate the cultivated *G. mangostana* var. *mangostana*, specifically identifies with their respective cultivation areas in West Java. These include (i) "*manggis Cengal*", (ii) "*manggis Puspahiang*" and (iii) "*manggis Wanayasa*".

In Sumatra, various local names are assigned to the cultivated mangosteen, including (i) "*manggis Ratu Tembilahan*" from Riau; (ii) "*manggis puting susu*", (iii) "*manggis curup*", (iv) "*manggis burik*", (v) "*manggis kutu*", (vi) "*manggis hijau*", (vii) "*manggis kuning*", (viii) "*manggis jumbo*" and (ix) "*manggis isi banyak / kipas*" from Bengkulu and Bangka-Belitung (Mansyah et al., 2007). The absence of references to herbarium specimens or deposited sequences in publicly accessible database for the aforementioned names impedes further research on these cultivated mangosteens due to the lack of referencing materials.

In North Kalimantan (Borneo), "*manggis Malinau*" likely represent a taxon differentiated from *G. mangostana*, as indicated by both morphological and phylogenetic findings (Santoso et al., 2019). While I have enumerated the aforementioned names from West Java, Sumatra and North Kalimantan, it is aknowledged that there may exist addintional vernacular names in these regions that remain localised and have not yet been scientifically documented. Moreover, some local names might potentially denote the same cultivated group. Notably, a comprehensive characterization of the morphological and genetic aspects of these cultivated groups is yet to be established.

1.1.3 The geographical distribution patterns and its determining factors

Cultivated mangosteen is extensively cultivated in Southeast Asia (**Figure 1.5**) including Indonesia, Malaysia, Thailand and Vietnam. In contrast, wild mangosteen varieties, namely var. *borneensis* and var. *malaccensis* are indigenous to Brunei, Indonesia, Malaysia and Singapore (**Figure 1.4**). The determination of the geographical distribution of these wild mangosteens varieties is imperative for the planning of sampling campaign.

To comprehend the distribution patterns of *G. mangostana* varieties, a thorough examination of contributing factors becomes essential. These factors emcompass climatic zones, biogeography, historic climate trends and the prevalence and extent of rainforests refugia. Investigating these elements is fundamental for gaining insights into the intricacies of the distribution patterns of *G. mangostana* varieties.

Southeast Asia (SEA hereafter) is divided into two major subregions: Mainland SEA and Maritime SEA. Mainland SEA is positioned in between India to the west and China to the northeast. Historically, Cambodia, Laos and Vietnam were collectively referred to as Indochina, a term now commonly used in the context of biogeography to encompass these three countries.

Maritime SEA is widely recognised as the Malay Archipelago. This region includes Peninsular Malaysia, and among its larger islands are Sumatra, Java and Sulawesi in Indonesia; Luzon, Mindanao, Samar and Palawan in the Philippines. Borneo Island, located at the centre of Maritime SEA, has international borders shared among three countries: Brunei, Indonesia (Kalimantan), and Malaysia (Sabah and Sarawak).

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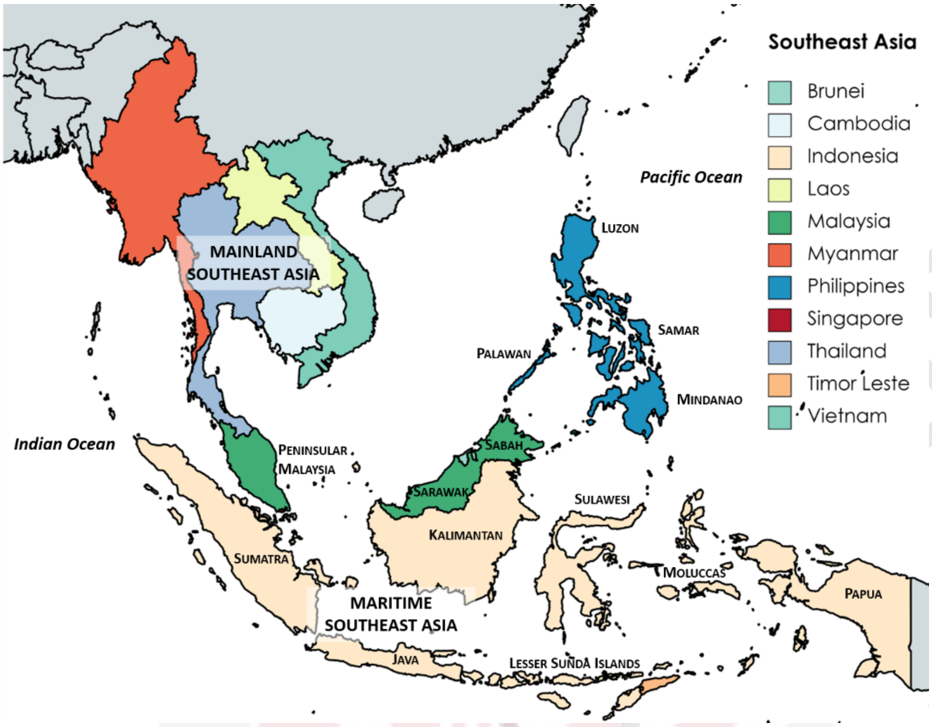

Figure 1.5 : Map of Southeast Asia. Southeast Asia comprises 11 countries that commonly categorised into Mainland Southeast Asia that comprises five countries: Cambodia, Laos, Myanmar, Thailand, Vietnam; and Maritime Southeast Asia that comprises six countries: Brunei, Indonesia, Malaysia, Philippines, Singapore, Timor Leste. Map created with mapchart.net

In accordance with the Köppen climate classification (Beck et al., 2018), noticeable distinctions in climate exist between Mainland SEA and Maritime SEA (**Figure 1.6**). Mainland SEA predominantly experiences a monsoon climate. Conversely, an equatorial climate prevails in Malaya, Sumatra and Borneo, coinciding with the natural distribution of *G. mangostana* wild varieties (**Figure 1.4**). In Java, equatorial climate is limited to a small area in the western part and the central highlands of the island, while monsoon and tropical savannah climates dominate other regions.

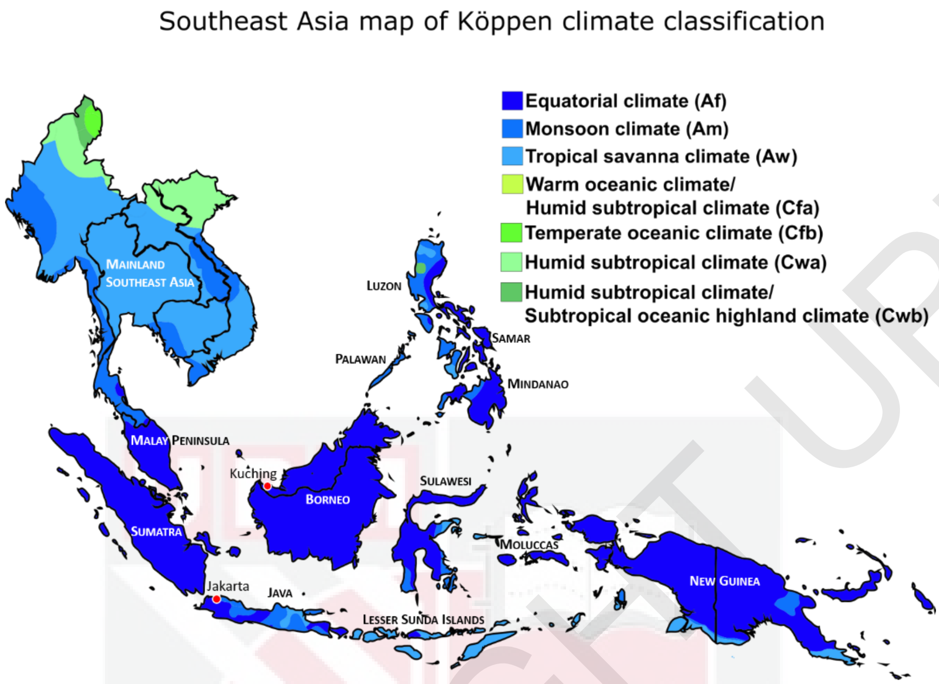

Figure 1.6 : Climate pattern in Southeast Asia (and Papua New Guinea) according to Köppen climate classification. Map downloaded from Wikipedia (Ali Zifan, 2016)

A significant distinction between equatorial climate and monsoon climate lies in the presence of a well-defined annual dry season in the area characterised by a monsoon climate, whereas equatorial climates lack a pronounced dry season. A dry season in Tropical Asia is identified by an average monthly rainfall below 100 mm for three consecutive months or more.

Illustrating this contrast, consider Jakarta, the capital city of Indonesia situated in northwest Java, which falls between equatorial and monsoon climate zones. Using Jakarta as an example, the annual precipitation is approximately 1700 mm, with average monthly precipitations falling below 50 mm for four consecutive months from July to October (WMO, 2023).

In contrast, Kuching, the capital of Sarawak in Northwest Borneo, located in the equatorial climate zone, exhibit a different pattern. The average annual rainfall in Kuching is slightly above 4000 mm, with July recording the lowest precipitation at about 185 mm. However, in the remaining 11 months, average monthly rainfalls range between 220–685 mm, exemplifying the consistent and comparatively higher precipitation levels in equatorial climates.

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The wild mangosteen varieties are restricted to evergreen rainforests in Sumatra, Peninsular Malaysia, and Borneo (Hambali & Natawijaya, 2016; Nazre et al., 2018). Field observations on the wild populations of var. *borneensis* revealed that these trees are typically situated along ephemeral streams in low-lying flat land (Yao et al., 2023).

It is noteworthy that cultivated mangosteen thrives in environments with minimal water stress, particularly during the seedling and sapling stages. In instances of dry seasons, irrigation may be necessary for survival (Osman & Milan, 2006). Therefore, one can infer that the mangosteen varieties in their natural habitats are predominantly found in regions devoid of a monsoon climate.

Malesia constitutes a botanical region encompassing Maritime SEA and New Guinea (**Figure 1.7**). The recognition of this region dates back to Heinrich Zollinger in 1857, with the concept subsequently refined and adopted by Cornelius van Steenis for "Flora Malesiana" project in mid twentieth century (Johns, 1995). Welzen et al. (2011) proposed the division of Malesia into three subregions: (i) the ever-wet Sundaland (Sunda), that comprises Sumatra, Malaya and Borneo; (ii) the Wallacea, encompassing Java, the Philippines, Sulawesi, Lesser Sunda Islands and Moluccas; and (iii) the New Guinea (Sahul). Welzen et al. (2011) also noted that Java Island straddles across Sunda and Wallacea floristic regions, reflecting the contrast between the flora in the ever-wet western part and areas with pronounced dry monsoon in the central and eastern parts. This regional division provides distinction of the subdivisions of flora within Malesia.

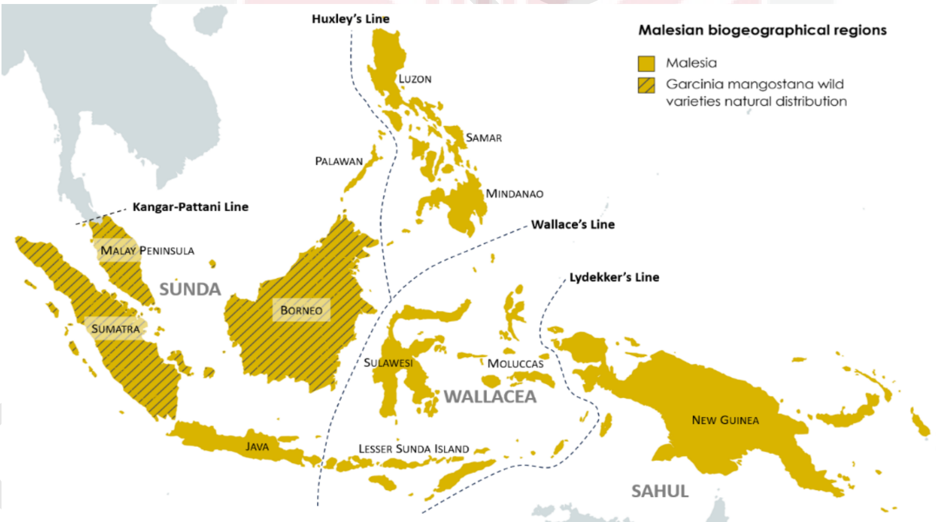

Figure 1.7 : Sub-biogeographical regions of the Malesia. Malesia is a floristic biogeographical region that comprises Maritime Southeast Asia and Papua New Guinea. Kangar-Pattani, Huxley's, Wallace's and Lydekker's Lines are the hypothetical biogeography boundaries proposed by naturalists based on their observations on faunistic and floristic distribution patterns. *Garcinia mangostana* varieties are naturally distributed in Malaya, Sumatra and Borneo. Base map created with mapchart.net

During past glacial maximums occurring approximately 17,000, 150,000 and 250,000 years before the present, when the sea level was about 120 m lower than the present sea level, two land masses appeared above sea level in the Malesia region, namely Sunda Shelf and Sahul Shelf (Voris, 2000), respectively labelled Sunda and Sahul in **Figure 1.7**. The islands in Wallacea remained separated by sea surfaces during these glacial periods.

Periodic unions of Malay Peninsula, Sumatra, Borneo, Palawan, Java and Bali occurred on the Sunda Shelf during past glacial maximums, facilitating the dispersal of plants, animals, and human migrations across the landmass. Flora and fauna occuring in the Sunda region are known as Sundaic elements, and the varieties of *Garcinia mangostana* are onsidered Sundaic elements.

However, the extent and distribution of the evergreen lowland forests were different during the last glacial maximum (LGM) (Cannon et al., 2009) (**Figure 1.8**). The lowland evergreen forest covered a substantial area currently submerged under the South China Sea, Java Sea and Strait of Malacca. When overlaying the extent and distribution of the evergreen lowland forests during the LGM on the current landmass, it can be inferred that the present Sundaic rainforests, especially in the lowland area of Sumatra, the Malay Peninsula, and Borneo, represent refugial dispersions of the past Sunda Shelf evergreen forests that migrated from adjacent areas now submerged.

Significantly, it is evident that the area where Java Island located was completely devoid of, and considerably distant from evergreen lowland rainforest during the LGM. This suggest that the predecessors of *G. mangostana* would not have survived in Java and adjacent areas during this period. Considering common factors influencing the distribution pattern of tree species such as current climate and historic vegetation distribution, one can infer that the natural distribution of wild *G. mangostana* varieties is confined to the evergreen Sundaic forests in Sumatra, the Malay Peninsula and Borneo, which are situated within the equatorial climate zone.

1.1.4 Breeding biology

Cultivated *G. mangostana* var. *mangostana* is a polyploid species primarily propagated asexually through seeds generated via adventitious embryogenesis. As a result, cultivated mangosteens exhibit uniform phenotypic appearance. The genotypes of these mangosteen, inclusive of heritable somatic mutations, remained stable across generations within cultivated lineages. The subsequent paragraphs provide a brief discussion of the key aspects of the distinctive breeding biology exhibited in cultivated mangosteen.

Dioecy is commonly observed in *Garcinia* species within the rainforests of Southeast Asia (Ha et al., 1988; Thomas, 1997). The presence of male trees in *G. mangostana* var. *mangostana* has been a subject of contention since the 1830s (Horn, 1940; King, 1890; Ridley, 1922; Roxburgh, 1832). Idris & Rukayah (1987) reported the identification of a male mangosteen tree in Peninsular Malaysia. They described the functional male

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flowers characterised by a stamens mass surrounding a pistillode. Although they detailed the morphology of the pollen grains and provided scanning electron microscope images, no information on their viability was furnished.

Staminodes are found in the functionally female flowers of mangosteen, where they produce no viable pollen (Lim, 1984). While labile sex expression is recognised in angiosperms (Käfer et al., 2022), the current understanding of *Garcinia* species is limited, hampering a comprehensive discussion. Scarce data are available regarding the sex ratio in wild populations of *Garcinia* species, with a notable lack of information on the sex ratio in *G. mangostana* var. *malaccensis* and var. *borneensis*.

Somatic embryogenesis in cultivated mangosteen was demonstrated over a century ago (A. L. Lim, 1984; Sprecher, 1919a, 1919b). The formation of asexual seeds in cultivated mangosteen results from adventitious embryo originating from a somatic cell of the ovary (Sprecher, 1919a, 1919b), and such asexual seed formation may be a common phenomenon in *Garcinia* species (Sweeney, 2008). While somatic embryogenesis is recognised as an efficient propagation pathway and is exploited in horticultural practices (Ramírez-Mosqueda, 2022), information regarding its natural occurrence is limited.

Hambali & Natawijaya (2016) successfully pollinated *G. mangostana* var. *mangostana* female flowers with var. *malaccensis* pollens in garden experiments. Their efforts resulted in obtaintion of viable seeds, which developed into triploid seedlings (Hambali & Natawijaya, 2016). These results show that mangosteen is a facultative apomictic species that is capable of sexual reproduction when a suitable source of viable pollen is available. From the same experiments, one knows that at least some var. *malaccensis* produce viable pollen.

In the case of *Mesta*, a cultivated variety of var. *malaccensis*, field observations and discussion with growers in Peninsular Malaysia indicated the likelihood of apomictic fruit production, given the apparent absence of male individuals in cultivation.

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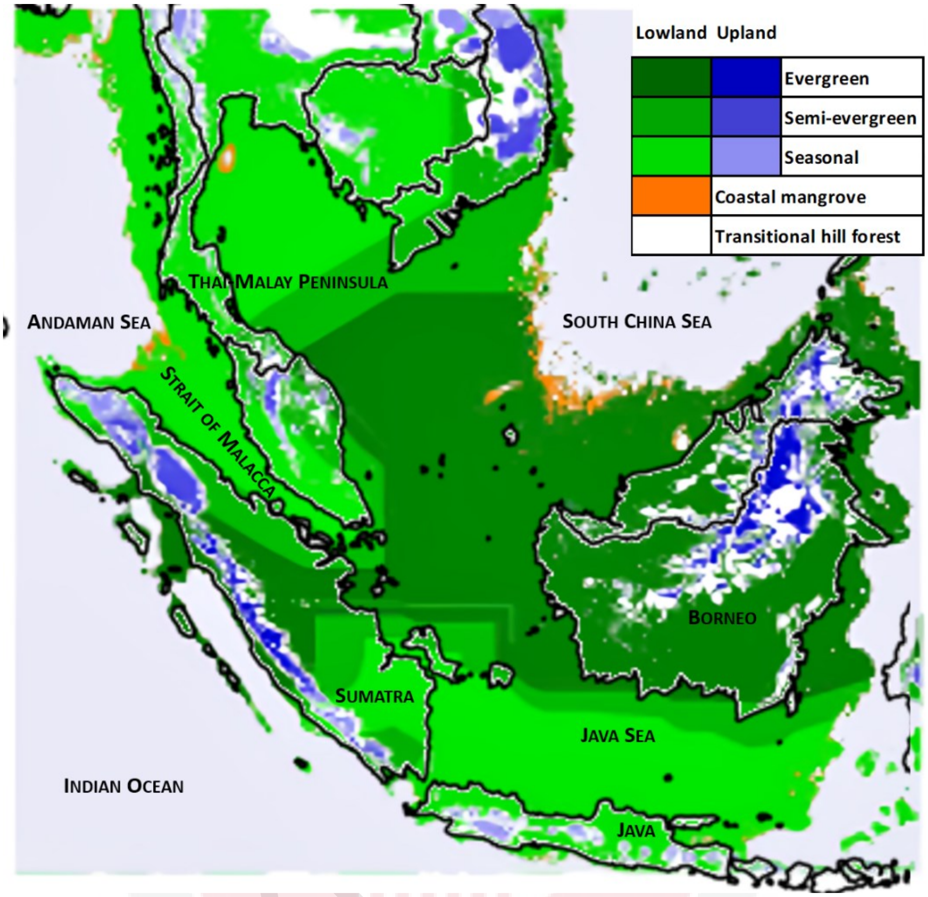

Figure 1.8 : Extent and distribution of vegetation types on Sunda Shelf during the Last Glacial Maximum as inferred from distribution modelling by Cannon et al. (2009). Adapted from Figure 1A, Cannon et al. (2009) depicting the maximum extent of evergreen vegetation model. Boundaries of the current land areas and labels of the regions are added

1.1.5 Polyploidy

The chromosomes of *Garcinia* present a challenge for enumeration due to their small size (Midin et al., 2018; Richards, 1990). Polyploidy has been identified in *G. mangostana* (**Table 1.2**): investigation reveal that var. *mangostana* is tetraploid (Matra et al., 2016; Midin, 2018), while diploids, triploids (Hambali & Natawijaya, 2016) and tetraploids (Midin, 2018) are observed in var. *malaccensis*. The chromosome number for var. *borneensis* remained unreported. Midin et al. (2018) demonstrated that dysploidy/aneuploidy in var. *mangostana*, revealing highly variable chromosome numbers ranging from 74 to 110 in an analysis of 20 metaphase spreads.

The maintenance of polyploidy in *G. mangostana* is facilitated by apomictic reproduction, mitigating potential difficulties with chromosome pairing during meiosis. Initial study proposed *G. mangostana* var. *mangostana* as alloploid (Richards, 1990), while subsequent studies categorise it as autoploidy (Hambali & Natawijaya, 2016; Nazre, 2014).

Table 1.2 : Chromosome counts in *G. mangostana* var. *mangostana* and *malaccensis*

var.	2n	Reference	Region
mangostana	*c*. 76	Krishnaswamy & Raman, 1949	Kerala, India
	96	Chennaveeraiah & Razdan, 1975; Tixier, 1960	India(?); Laos
	c. 88–90	Ha, 1978	Pen. Malaysia
	96	Hambali & Natawijaya, 2016	Java
	74–110	Midin, 2018	Pen. Malaysia
malaccensis	48, 72	Hambali & Natawijaya, 2016	Sumatra

1.2 Fruit tree domestication

1.2.1 Domestication: a bird's eye view

The domestication of plants and animals stands as arguably the most significant revolution of human history, propelling the emergence of human civilizations and, ultimately, shaping the contemporary world in which we live today (Diamond, 2002). Domesticated plants and animals have bestowed upon humankind a more stable and reliable food supply. Additionally, the domestication of animals also provided humans with transportation, labour, and companionship. Domestication practices exemplify how humans coexist and engage with the natural world, particularly in terms of modifying the natural environment and mananging biological diversity. Over the past 12,000 years, humans have brought thousands of plant species into domestication (Meyer & Purugganan, 2013).

In the realm of plant domestication, early written texts addressing useful plants and their cultivation trace back to classical antiquity, exemplified prominently by "Historia plantarum" (Theophrastus, 1916), written in between c. 350–287 BCE. Another seminal work, "The origin of cultivated plants" (de Candolle, 2011 [originally published in 1886]) culminated from the first systematic investigation into plant domestication at a global scale. "Origin and Geography of Cultivated Plants" (Vavilov & Dorofeev, 1992) signified the importance of genetic diversity for crop improvement, influencing the subsequent breeding programmes and the development of high-yielding, disease-resistant crop varieties. These publications laid the groundwork for understanding the origins, diversity, and conservation of cultivated plants, as well as their significance for global agriculture.

In recent decades, the field of archaeobotany and genetic studies has witnessed significant advancements, contributing profound insights into the origin and dissemination of agriculture and crops. Concurrently, the acceleration in the loss of

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traditional landraces and wild relatives, has resulted in a drastic decline in agrobiodiversity. Against this backdrop, Harlan (1992) undertook the task of synthesing these developments in “Crop and man”, thereby presenting a comprehensive perspective on the relationship between humans and crops. The work intergrates findings of anthropology, archaeology, botany, and agronomy, employing an interdisciplinary approach to illuminate various facets of this dynamic interaction.

Harlan's work not only serves as a bridge between diverse academic disciplines but also furnishes vivid examples illustrating how various socio-cultural human societies have actively influenced crop diversity and the evolving landscapes of agriculture over time. Furthermore, the author underscores the significance of crop diversity as an indispensable resource for ensuring food security and promoting agricultural sustainability. In doing so, Harlan's synthesis emerges as a crucial resource for scholars and researchers seeking a nuanced understanding of the intricate interplay between humanity and the cultivation of crops.

From the perspective of contemporary scientific inquiry, domestication is defined as an evolutionary process characterised by directional selection of traits that are favourable to humans (Kantar et al., 2017). In elucidating this phenomenon, the “modern synthesis” offers a robust conceptual framework, particularly in examination to study the population genetics concerning domesticated plants and animals (Zeder, 2017).

The modern synthesis represents an integrative approach that combined insights from various disciplines, including anthropology, archaeology, evolutionary biology, genetics and phenotypic changes. This comprehensive methodology aims to elucidate the process of domestication by scrutinising the transformations undergone by plants and animals during their transition from wild to domesticated forms. Utilizing archaeological studies, researchers uncover samples that facilitate the interpretation of phenotypic changes in the domesticates. Moreover, these archaeological samples serve as a source of DNA materials for conducting ancient DNA analyses (Zeder et al., 2006).

In instances of exceptional circumstances, researchers may acquire resurrection DNA by geminating ancient seeds found at archaeological sites, thereby enabling in-depth genetic studies (Gros-Balthazard et al., 2021). Within the realm of genetics, ongoing advancements in DNA sequencing and genetic analysis technologies have empowered researchers to compare the genomes of wild and domesticated species. This comparative analysis is instrumental in deducing the domestication history, as demonstrated in the studies examining apricot (Groppi et al., 2021), olive (Besnard et al., 2013) and pears (Yue et al., 2018). These scientific endeavors showcase the pivotal role played by modern genetic tools in unraveling the complex narrative of domestication across various plant and animal species.

In instances where ancient DNA from the progenitors is accessible, researchers can conduct genomic comparisons between these ancestral specimens and contemporary cultigens (Cappellini et al., 2010; Cohen et al., 2023). This comparative analysis, which involves assessing the genetic material of both wild and ancient progentiors alongside that of cultigens, serves as a tool for identifying specific genes or genomic regions that

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have undergone selective changes during the process of domestication. Such investigations provide crucial insights into the molecular basis of domestication.

Although domesticated plants benefit human in various ways, the domestication processes, particularly those involving selection and adaptations to man-made environments, have led to a reduction in genetic diversity within cultigens (Smýkal et al., 2018). The intentional breeding and cultivation practices have often favored specific traits, resulting in a narrowing of the genetic variation present in domesticated crops. This reduction in diversity can have implications for the resilience and adaptability of cultivated species in the face of environmental challenges.

Conversely, wild relatives of domesticated plants serve as a genetic reservoir for cultigens, harboring a reservoir of potential genes that can contribute to crop improvements and enhance adaptability (Majeed et al., 2021). The genetic diversity found in wild relatives represents a valuable resource for breeding programs, offering a pool of traits that may resist pests, diseases, and environmental stresses. Therefore, understanding and preserving the genetic diversity present in wild relatives is essential for ensuring the long-term sustainability and resilience of domesticated crops.

The modern synthesis serves as a solid foundation for exploring the origins and genetic constituents of domesticates species, especially in the case of understudied tropical fruit trees such as the cultivated mangosteen, which is the focal of the present study. In the subsequent sections, I delve into topics pertinent to fruit tree domestication, with a specific emphasis on tropical regions. This investigation aims to contribute to our understanding of the complex processes involved in the domestication of tropical fruit trees.

1.2.2 The domestication of fruit trees

The early domestication of fruit trees is well exemplified by the cultivation of fig (*Ficus carica* L.) and olive (*Olea europaea* L.) in the Near East (Zohary & Spiegel-Roy, 1975), as documented in early records dating back to 3000–2000 and 2000–1000 BCE, respectively. Beyond the near east, citruses such as *Citrus aurantium* L. and *C. maxima* (Burm.) Merr. were domesticated in China before 2200 BCE (Spiegel-Roy, 1986) and the cultivation of mango (*Mangifera indica* L.) is noted to have started around 2000 BCE in the Indian subcontinent (Mukherjee, 1972).

Domestication syndrome is generally defined as a suite of traits that characterise a divergence from the wild progenitor(s) in domesticated plants. This suite comprises traits desirable to humans, though not necessarily beneficial to the plant (Meyer et al., 2012). A review on the domestication syndrome in historically cultivated fruit trees highlighted specific trait changes compared to their wild progenitors. Notable major changes include self-fertility in peach and sour cherry, the elimination of bitterness in almond nuts, reduced resin content in mango fruits, and the development of thornlessness in citruses (Spiegel-Roy, 1986). However, the review emphasized these trait changes in

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domesticated fruit trees, in comparison to their progenitors, may not always be pronounced.

Unlike domesticated annuals, especially grain crops, tree crops often exhibit fewer domestication syndromes. An analysis of major and minor crops over domestication time. encompasing species (Kantar et al., 2017), included only two fruit tree crops: olive and Brazil nuts (*Bertholletia excelsa* Bonpl.). Olive and sunflower were introduced into domestication around the same period. However, while six domestication syndromes are recognised in sunflower, only two are identified in the case of olive. The longer generation time of tree crops emerges as an obvious factor contributing to this disparity.

In the context of genetic considerations, domesticated perennial fruit crops exhibit weaker genetic bottleneck, retaining approximately 95% of the ancestral genetic variations. This contrast with annual fruit crops, which retain only around 60% of the original genetic diversity (Miller & Gross, 2011). The genetic profile of perennial fruit crops is also enriched through sexual reproduction cycles and the fixation of somatic mutations in clonal cultivars (Gaut, Díez & Morrell, 2015).

1.2.3 Domestication of fruit tree in the tropics

Harlan (1971) recognised four regions of agricultural origin across the tropical belt, as illustrated in **Figure 1.9**. These include three 'non-centres': (i) African (A2), (ii) Southeast Asian and South Pacific (B2), and (iii) South American (C2). Additionally, there is the Mesoamerican 'centre' (C1). Notably, among the widely cultivated species of fruit and nut trees, such as *Artocarpus* spp. (breadfruits), *Citrus* spp. (citruses), *Mangifera* spp. (mangoes), *Nephelium* spp. (rambutans) and *Syzygium* spp. (wax apple), their origins can be traced back to Southeast Asia and South Pacific.

Emblematic fruit tree species of tropical America origin include *Bertholletia excelsa*, *Theobroma cacao* L. (cacao), *Pouteria caimito* Radlk. (abiu), *Inga edulis* Mart. (ice-cream bean) and *Pourouma cecropiifolia* Mart. (Amazon tree-grape). Their traces of domestication are evidenced by being hyper-dominant in Amazonian forests, particularly in the vicinities of archaeological sites (Levis et al., 2017). These species also exhibit a broader distribution than other dominant species, suggesting human mediated dispersal.

In addition to the aforementioned iconic fruit tree species, numerous other species are cultivated in the tropics for fruits and nuts (Clement, 1999), with their cultivation status spanning a continuum from incipient change to fully domesticated. The survival of these species is entirely dependent on the intervention of farmers (Clement et al., 2015). Due to their reliance on human tending, serious genetic diversity loss occurred in these fruit tree species during the drastic human population decline in the Amazonian forests around 1500's (Clement, 1999), attributed to Portuguese and Spanish colonisation. The population decline was so severe that some settlements were completely wiped out, leaving the domesticated trees unattended and eventually decimated. Recent forest degradation (Escobar, 2019) has further exacerbated the loss.

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Among the tree crops originating from tropical Africa, *Coffea arabica* L. and *C. canephora* Pierre ex A.Froehner are perhaps the most extensively studied global commodities concerning their origin and genetic diversity (Bawin et al., 2021; Davis et al., 2023; Ngugi & Aluka, 2019). Nevertheless, the domestication of other fruit tree species in Tropical Africa has remained understudied despite their socioeconomic significance (Rimlinger et al., 2019). *Dacryodes edulis* (G.Don.) H.J.Lam (*safoutier*, African plum), an iconic species with an oily endocarp eaten as a vegetable, is relatively well-studied. Human selection has revealed a domestication syndrome, including a higher percentage of male and male-hermaphrodite sexual types in the wild compartment and a lower fruit and seed mass in wild individuals compared to cultivated ones (Mboujda et al., 2022). Highly variable and transferrable microsatellites have been developed to investigate the population structure of the species (Rimlinger et al., 2020).

Cola nuts (*Cola acuminata* (P.Beauv.) Schott & Endl. and *C. nitida* (Vent.) Schott & Endl.), and seed of *Garcinia kola* Heckel are used as stimulant. Research into their genetic diversity and domestication is still in its infancy (Yogom et al., 2023).

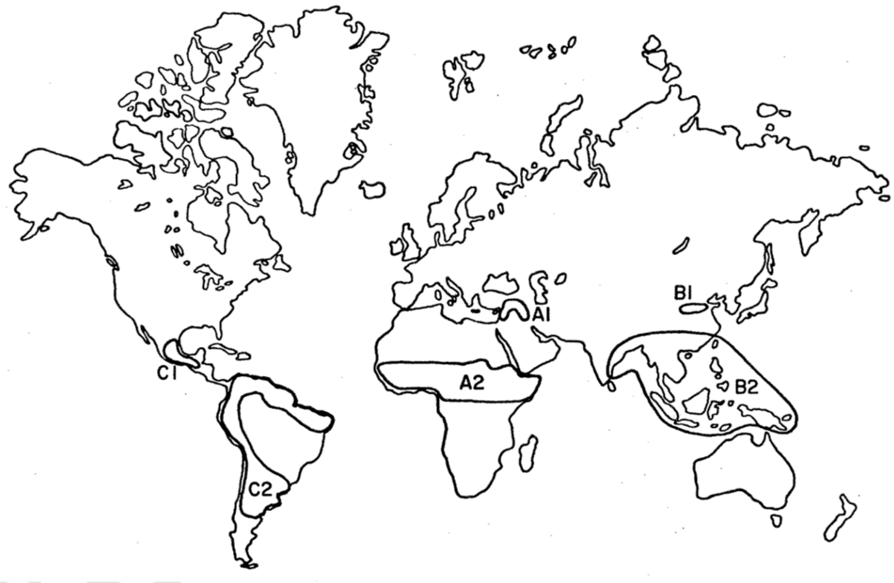

Figure 1.9 : Map depicting Harlan's centres and non-centres of agricultural origins (adapted from Figure 6, Harlan, 1971). A1, Near East centre; A2, African non-centre; BI, North Chinese centre; B2, Southeast Asian and South Pacific non-centre; CI, Mesoamerican centre; C2, South American non-centre

In contrast to the major fruit tree species in Eurasia such as apple and pears, which dispersed over vast land areas, sea routes play a crucial role in the spread of tropical fruits. Breadfruit (*Artocarpus altilis (Parkinson) Fosberg*) is recognised to have been disseminated through human migrations between archipelagos in the Pacific Ocean (Zerega et al., 2004). Among the three tropical regions, transregional exchanges of many of these fruit tree species occurred during the early part of the Age of Exploration, particularly through the efforts of the Portuguese and Spanish (Blench, 2007).

In contemporary times, approximately 2700 species of tropical fruits are available in marketplaces. These fruits not only serve as an important source of nutrition for the local populations but also contribute to the incomes for farmers engaged in production for export markets (FAO, 2023). Noetworthy is the fact that nearly 99 % of tropical fruit production originates in developing countries, playing a vital role in sustaining local subsistence economies and livelihoods.

1.2.4 Domestication of fruit trees in Southeast Asia

Cultivated mangosteen and its wild relatives originated in Southeast Asia. Hence, the domestication of fruit trees in Southeast Asia is explored in a more in-depth manner. I have considered topics across broader aspects to offer a comprehensive perspective for the current study.

1.2.5 Exceptional diversity in edible fruit species

The lowland forests in Southeast Asia host an extraordinary diversity of edible fruit tree species (Harlan, 1992). An exploration into the species composition of a 50-ha permanent tree demography plot at Pasoh, Negeri Sembilan, Peninsular Malaysia provided insight into the diversity of edible wild fruits (Saw et al., 1991). The study revealed that several genera are especially species-rich such as *Artocarpus* (Moraceae) with 10 species; *Garcinia* (Clusiaceae) with 13 species, *Mangifera* (Anacardiaceae) with 12 species, and *Nephelium* (Sapindaceae) with 5 species. These invaluable natural resources gave rise to many of the fruits that have already been brought into cultivation and continue to serve as a potential reservoir of agrobiodiversity.

A comprehensive compilation of edible fruits and nuts occuring in Southeast Asia is presented in the “Edible Fruits and Nuts” in the “Plant Resources of South-East Asia” series (Verheij & Coronel, 1991). This compendium features 120 major species with detailed monographs and illustrations in line drawings, along with summary information an additional 275 minor species.

1.2.6 Paucity of historical and archaeological records

The historical textual record on plant domestication in Southeast Asia is sparse. Contacts between the region and Indian and Arabian traders through the Indian Ocean Trade routes date back to ancient times. However, it was not until the early 15th century that the first written records of natural products with explicit details of the locations appeared (Ma, 2019 [1416]). Blench (2007) employed a linguistic approach, analysing loanwords to infer the routes of the spread of fruit cultivation in mainland Southeast Asia. Linguistic analyses suggest common exchanges of fruits between Southeast Asia, India and China.

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However, many characteristic Southeast Asian fruits have only recently spread beyond the region.

Similarly, archaeological findings recovering food residuals, especially fruits, are limited (Paz, 2005). Traces of starchy vegetables and spices, such as sago, purple yam and nutmeg, were evident on potsherds dated around 1500–300 BCE, excavated from an archaeological site in Pulau Ai, South Moluccas, Indonesia (Lape et al., 2018). Charred rind fragments of citrus fruits were recovered in flotation samples dated around 400–1 BCE at Khao Sam Kaeo, Peninsular Thailand (Fuller et al., 2018). Among local fruits, durian (*Durio zibethinus* L.) and jackfruit (*Artocarpus* spp.) produce edible seeds covered by a thin seed coat. These factors limit archaeobotanical record of persevered seeds. In contrast, hard protective structures, such as the endocarps enveloping the seeds of *Canarium* and *Terminalia* species, are more likely to be found as charred archaeological plant macrofossils (Fairbairn & Florin, 2022).

1.2.7 Developmental pathways of fruit tree domestication and fruit production

When studying the developmental pathways of fruit tree domestication and fruit production in the region, two key points to consider. Firstly, the fruiting onset is a crucial factor. Well-tended trees in modern cultivation only begin to set fruit at seven year-old in both durian (National Research Council, 1975) and mangosteen (Almeyda & Martin, 1976). The initial planting stocks intorduced into cultivation by early cultivators would require an even longer period.

Secondly, the adaptability of fruit trees seedlings and saplings to establish themselves in man-made environments is significant. Using durian and mangosteen as examples once again, their seedlings and saplings exhibit shade tolerance and would not survive without intensive care in a man-made environment. In contrast, the natural environment of a pristine forest with a closed canopy and high humidity proves ideal for the survival and growth of seedlings and saplings.

The cultivation of trees with a delayed onset of production represents a substantial long-term investment. The husbandry practices involving the introduction of forest species into a human modified environments, as outlined by Wiersum (2008) (**Table 1.3**), were likely inculcated through heuristic learning among early cultivators. Wiersum (2008) framed the outline of mutual developement between production systems and cultivated trees into phasic orders. These phasic orders advance along a gradient of increasing management intensity, emphasising the coevolution of niches and cultivated trees. Wiersum's framework was formulated with specific reference to Southeast Asian scenarios, supported by examples from the Neotropics (Anderson, 1990).

The progression unfolds as follows: initially, local communities gathered fruits from wild trees in the natural forests. This was followed by a gradient of forest management regimes aimed at enhancing the presence of fruit trees and increasing fruit yield. Ultimately, cultigens were introduced into man-made environments (**Table 1.3**). These

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phases differ in the intensity of human intervention and the environment settings involved.

Table 1.3 : Phasic framework of mutual progress between production systems and cultivated trees in exploitation of tree crops; after Table 4.2

Phase	***modus operandi***
I. Acquiring of wild tree products by gathering/collection	range from uncontrolled, open access gathering of forest products to controlled gathering of wild tree products
II. Initial production of wild tree products	range from systematic collection of wild tree products with protective tending of valued tree species to selective cultivation of valued trees by artificial *in situ* regeneration of native tree
III. Cultivation of wild trees	cultivated of selected native tree species in artificially established plantations
IV. Cultivation of fully domesticated trees	cultivation of genetically selected or improved tree crops in intensively managed plantations

(Adapted from Wiersum 2008)

1.3 Research problems and plausible solutions

1.3.1 The origin of the cultivated mangosteen: a contentious conundrum

The origin of the cultivated mangosteen has been a contentious topic for decades, marked by incongruous findings from cytological and phylogenetics studies. Candidate progenitors, including *Garcinia celebica*, *G. diospyrifolia*, *G. mangostana* var. *malaccensis* and *G. penangiana* have been proposed in various studies (Richards, 1990; Abdullah et al., 2012; Nazre, 2014). More recent findings, particularly from Hambali & Natawijaya (2016) and Nazre (2014), suggest that var. *malaccensis* is the most probable sole progenitor of the cultivated mangosteen.

Despite there previous studies, there has been limited study on *G. mangostana* var. *borneensis*, especially its genetic affinity to var. *mangostana*. The inclusion of *G. mangostana* var. *borneensis* in this study is, therefore, indispensable to clarify the tokogeny between *G. mangostana* varieties.

Nazre (2014) and Hambali & Natawijaya (2016) have provided indications on how the cultivated mangosteen emerged from var. *malaccensis*, but the overview of its domestication history remains incomplete. *Garcinia mangostana* var. *malaccensis* exhibits distribution throughout the Malay Peninsula, Sumatra and West Borneo. However, a crucial question arises: does the domentsitcation history in mangosteen show any geographical-signal? For example, *G. mangostana* var. *borneensis* is restricted to East Borneo, particularly common in the east coast of Sabah. Are the mangosteens cultivated in East Borneo more closely related to var. *borneensis* when compared to var. *malaccensis*? Alternatively, did the modern cultivated mangosteens originate from a few

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polyploid apomictic ancestors in a particular region, and was the lineage propagated and disseminated through human-mediated dispersal? These questions, as of now, remained unanswered.

Considering the effects of domestication syndrome on the breeding biology, particularly apomixis in mangosteen, Yao et al. (2023) have proposed an evolutionary-ecological theory named "Forest-*Dusun* Interface" (**Figure 1.10 & Chapter 2**), which aligned with Wiersum's (2008) phasic framework. In this context, "*Dusun*" (Malay) refers to subsistence orchards. The Forest-*Dusun* Interface presents two possible scenarios.

In the first scenario, apomixis evolved during domestication. Upon the initial and unbiased introduction of planting stocks into the man-made environments, the culling of individuals that did not bear fruits might have occured, leading to the positive selection of apomictic females. Polyploidy might have evolved concurrently with or independently of apomixis. The second scenario is simpler: apomixis and polyploidy were already present in wild progenitors and were introduced into cultivation by the early cultivators.

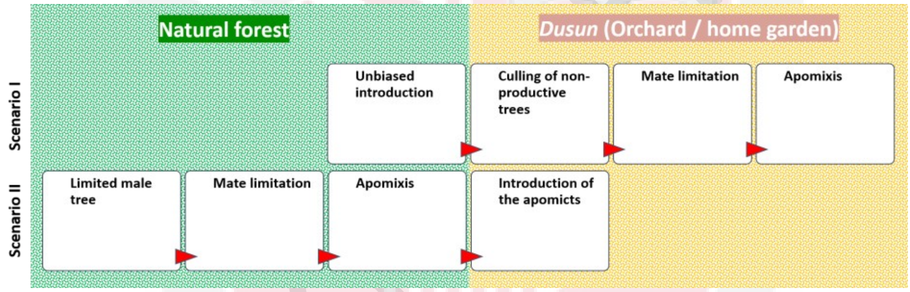

Figure 1.10 : Forest-*Dusun* Interface. This evolutionary-ecological theory put forward two possible scenarios regarding the inception of apomixis reproduction and polyploidy in cultivated mangosteen

1.3.2 Deducing the domestication history: suitable approaches for *G. mangostana*

The current understanding of the cultivated mangosteen and its wild relatives prompts new consequential research questions:

1) Is the varietal delimitation of the cultivated and wild varieties well defined based on morphological characters?
2) What is the intraspecific tokogeny between the cultivated populations and wild relatives?
3) Given that var. *malaccensis* is distributed in Sumatra, Malay Peninsula and western Borneo, and var. *borneensis* is distributed in eastern Borneo, is there

a recoverable geographical signal between the cultivated populations and the wild relatives in these respective regions?

Addressing these questions will contribute to a more comphrehensive understanding of the mangosteen's domestication history, varietal distinctions, and the relationships between cultivated and wild populations across different geographical regions.

Several methods are commonly emplyed to trace the domestication history of a cultivated trees. These methods, as outlined by Herniter et al. (2020) and Warschefsky & von Wettberg (2019), include (i) archaeobotanical studies; (ii) examination and interpretation of historical records; (iii) ethnobotanical surveys; (v) morphological analyses and (v) genetic analyses.

Realistically, a combination of methods, tailored to the available data and research context, is often the most effective approach. Integrating findings from multiple sources can provide a more comprehensive understanding of mangosteen's domestication history.

1.3.3 Archaeobotanical study

Archaeobotanical studies involve the analysis of plant remains preserved, and recovered from archaeological sites. The examination of the carbonised or charred plant remains, such as ancient stony seeds and hard fruits capsules, allows researchers to identify and compare morphological characteristics of the ancient domesticated species with modern domesticated species and their wild relatives. By interpretating these findings, researchers can infer when and where the domestication originated. Unfortunately, representations of plant remains, especially tree fruit, in archaeobotanical studies of Southeast Asia are scarce and restricted to a few species (Fairbairn & Florin, 2022; Paz, 2005). Regrettably, to date, archaeobotanical approaches have not provided any information on the cultivation history of mangosteen.

1.3.4 Examination and interpretation of historical records

Examination and interpretation of historical records, such as ancient texts, manuscripts and illustrations such as cave paintings and ancient building reliefs, offer insightful information into the domestication history of species. These records may describe cultivation practices, natural products available in the marketplace, trade routes, and the cultural significance of specific domesticated trees. Such information provides useful insights into the timeline of domestication and the geographical spread of domesticated tree species.

In the case of Southeast Asia, historical texts on the geography, culture and natural products often find their first records in Chinese texts (Gong, 2019 [originally published in 1434]; I-ching, 1896 [originally written between 671–695]; Ma, 2019 [originally published in 1416]). These historical texts are written in archaic languages and can be

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difficult to interpret without translated, or annotated versions. Historical records suggest that mangosteen was among the fruits sold in the marketplaces in East Java and North Sumatra (Gong, 2019; Ma, 2019). However, there is no indication of whether the fruits were collected from forests or cultivated in orchards or home gardens (Yao et al., 2023).

1.3.5 Ethnobotanical survey

Ethnobotanical surveys are invaluable for gathering information on cultivation practices, providing insights into the selection of desirable traits (McKey et al., 2010). Recent ethnobotanical studies conducted in Southeast Asia have primariliy focused on the tree structure and species composition of the agroforests and home gardens (Aumeeruddy, 1993; Michon et al., 1983, 1986). In contrast, older studies such as Freeman (1955) focused on grain crops such as hill rice. However, as of my best knowledge, I am not aware of any specific ethnobotanical study in the region that specifically focuses on how farmers' practices shaped the variation in fruit tree produce, as exemplified in Rimlinger et al. (2019).

1.3.6 Morphological analysis

Morphological analyses serve as the initial steps in identifying the probable wild relatives of a cultivated species, providing a direct observation on phenotypes. Through comparisons on morphological traits in vegetative (twigs and leaves) and reproductive organs (flowers and fruits) between the domesticated and wild populations, researchers can identify changes that occurred during domestication, characterizing the domestication syndrome. Botanical institutes offer excellent opportunities for conducting morphological studies.

Herbarium specimens of *G. mangostana* wild relatives are well-represented in regional herbari, including Kepong, Forest Research Institute Malayia (KEP); Sandakan, Forest Research Centre, Sabah (SAN); Singapore, Singapore Botanic Garden (SING); and Wanariset, Balai Penerapan Standar Instrumen Lingkungan Hidup dan Kehutanan Samboja, East Kalimantan (WAN). Geographical distributions and morphological variations of var. *malaccensis* and var. *borneensis* are primariliy documented through herbarium records. Unfortunately, the full range of variations in cultivated mangosteen is not comphrehensively represented in herbaria.

1.3.7 Genetic analysis

Genetic analyses play a crucial role in tracing the domestication history of cultivated species. Depending on the availability of reference genomes and the selection of the genetic markers, researchers can address different research questions. Presently, high-throughput next-generation sequencing technologies enable the generation of large datasets of Single Nucleotide Polymorphisms (SNPs) at a manageable cost. Simple Sequence Repeats (SSRs) continue to be an effective marker for examining population genetic variation.

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By comparing SNPs and SSRs between populations of cultivated and wild relatives, researchers can characterise population genetic variation and identify genotypes. This information aids in understanding the relationships, diversity, and evolutionary dynamics between cultivated and wild populations, contributing to a more comprehensive understanding of the domestication history of the species in question.

The chloroplast genome is known for its higher conservation in both gene content and physical structure compared to nuclear and mitochondrial genomes (Jansen et al., 2005). The nucleotide mutation rate of chloroplast genes is moderate, falling between the rates of nuclear and mitochondrial genes (Dong et al., 2020). Chloroplast markers have long been proven suitable for inferring the population tokogeny of different plant groups (D. E. Soltis et al., 1992) and enable the differentiation of lineage sorting from polymorphic ancestry (Lavin et al., 1991).

Studies by Miller & Schaal (2005) and (Yue et al., 2018) successfully identified haplotypes in fruit tree species using chloroplast markers. These studies were able to infer the domestication history and geographical origin of cultivated fruit. Additionally, the chloroplast genome is maternally inherited, haploid and non-recombining (Birky, 2001). These characteristics makes chloroplast genome SNPs ideal markers for reconstructing the demographic history of plant species.

Given the scarcity of archaeobotanical findings, historical records, and ethnobotanical studies focused on cultivated trees in Southeast Asia, the adapotion of comparative morphological and genetic studies appeared as the most viable and realistic approaches for the current study

1.4 Objectives

The overarching goal of this study is to deduce the domestication history of the cultivated mangosteen and contribute to the conservation, sustainable management, and utilisation of genetic resources in both cultivated and wild mangosteen populations. The specific objectives identified to achieve this overarching goal are outlined below:

(I) To clarify the relationship between and within the cultivated mangosteen and wild relatives through morphological and genetics studies;

(II) To elucidate the origin of domesticated and evolutionary history of cultivated mangosteen through genetic analyses;

(III) To characterise the geographical distribution of genetic diversity among the wild populations for the formulation of conservation plan.

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1.5 Thesis work plan

The current study adopts a multiple-faceted approach, incoporating both botanical and genetic methods, to fulfils its objectives. **Chapter 2** presents an extensive literature review with a specific emphasis on the origin of cultivated mangosteen and its breeding biology. This review aids in establishing a coherent theoretical framework and defining the geographical boundaries for sampling. The sampling scope, and overview of morphology and genetic studies, are outlined below.

1.5.1 Sampling campaign plan

Given the postulation from previous studies that the cultivated mangosteen originated in a region spanning across Sumatra, Peninsular Malaysia, Singapore and Borneo, strategic sampling efforts are essential. To elucidate the origin of cultivated mangosteen and gain a comprehensive perspective of the domestication history, sampling should cover populations across Indonesia, Malaysia and Singapore. This geographical approach aims to capture the diversity of mangosteen populations within the suggested origin region.

In term of taxonomic representation, it is crucial to conduct sampling not pnly of cultivated mangosteen across the region but also of its wild relatives, namely *G. mangostana* var. *borneensis* and var. *malaccensis* are needed. This inclusive approach ensures a thorough examination of the entire species complex, facilitating a more accurate analysis of the relationships between cultivated and wild mangosteen populations.

Sampling of the cultivated *G. mangostana* var. *mangostana* and var. *malaccensis* from orchards and agricultural centres represents a relatively easy task. However, the challenge lies in the sampling of wild relatives, especially in acquiring at least 20 individuals per population for population genetic study. Wild populations of *G. mangostana* var. *borneensis* and var. *malaccensis* are located in remote forested areas. Locating and collecting them is logistically challenging. Additionally, obtaining the necessary permissions for fieldworks across the entire region add another layer of complexity. Extracting leaf tissues from herbarium specimens is an alternative sampling method for the wild relatives.

Species of congeners, especially in the *Garcinia* sect. *Garcinia* are also collected when they were encountered during the fieldworks. Additionally, other *Garcinia* species not native to Southeast Asia were collected from botanical gardens, agriculture centres, and private gardens. In total, the study gathered 545 accessions of leaf tissues. These accessions, obtained from both field collections and the extraction of tissues from herbarium specimens, cover the entire region of origin. The localities of all samples gathered in this study are mapped in **Figure 1.11**.

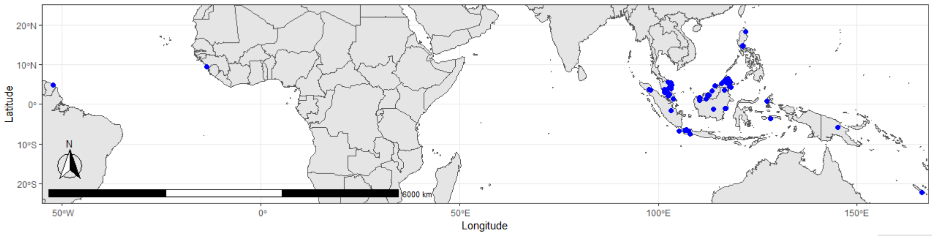

Figure 1.11 : The distribution of all samples acquired for this study

Field trips were conducted for three main purposes: (i) to supplement herbarium specimens intended for morphometric analyses; (ii) to make observations on field characters and niche preferences; and (iii) to collect leaf tissues for subsequent genetic analyses. The sampling fieldwork spanned various countries and regions, specifically Peninsular Malaysia, Singapore, West Java, Sabah and East Kalimantan. The sampling coverage of the two wild varieties is mapped in **Figure 1.12**. It is crucial to emphasize that the majority of the collected accessions originated from sterile trees encountered during the fieldwork. Additionally, some specimens were obtained from young saplings, and attempts to locate the supposed mother trees were unsuccessful. Consequently, the taxon identification of these samples relied on vegetative characters.

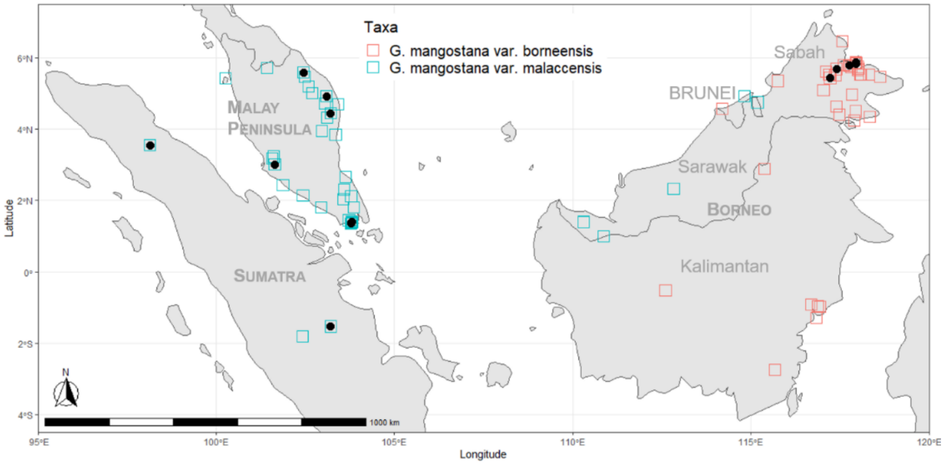

Figure 1.12 : The sampling coverage of two wild varieties. The bullets (•) denote the sites where samples were acquired for this study. Note that the Sumatran samples were collected *ex-situ* from private gardens in West Java

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1.5.2 Morphometric analyses

Cultivated mangosteens were classified under *G. mangostana* var. *mangostana*, while var. *malaccensis* and var. *borneensis* were recently defined to accommodate the two wild relatives (Nazre et al., 2018). However, the morphological characters used to delimitate these two new taxa have not undergone rigorous statistical analyses to assess their efficacy. In order to clarify the varietal distinction within *Garcinia mangostana* and distinguish them from from two other morphologically similar species, namely *G. penangiana* and G. *venulosa*, morphometric analyses were employed. A total of 124 specimens were examined, including *G. mangostana* var. *mangostana* (35), var. *borneensis* (16), var. *malaccensis* (23), *G. penangiana* (30) and *G. venulosa* (20). The results of the morphometric study, outlined in **Chapter 3**, are essential for determining whether the morphplogical phenotypes align with the genotypes. These findings would contribute to validating the consistency between morphological phenotypes and genetic makeup.

1.5.3 Genetics: phylogenomic and population genetic approaches

Laboratory work was conducted at "Plant Biodiversity and Adaptation Research Group (DYNADIV)" plant genetics laboratory in *Institut de Recherche pour le Développement* (IRD), Montpellier, France.

A total of 192 samples were chosen for genetic library construction. The High-seq Illumina technology was employed to conduct the sequencing of the genetics datasets. The two datasets generated from the library encompassed: (i) untargeted whole genome sequencing (WGS) sequences, and (ii) targeted sequencing using universal Angiosperms353 probes. In case of WGS sequences, alignment with a published chloroplast genome facilitated the identification of Single Nucleotide Polymorphisms (SNPs) from the mapped sequences. The chloroplast genomic SNPs were instrumental in unraveling the phylogenetic relationships among all studied taxa, as well as elucidating haplotypes within cultivated and wild mangosteen populations. The genetic study is presented in **Chapter 4**.

Notably, at the time of thesis submission, the bioinformatics analysis of the Angiosperms353 dataset had been completed up to the re-paring stage. The presence of polyploidy in cultivated mangosteen necessitated the implementation of more technically-demanding and time-consuming procedures to eliminate paralogs. Consequently, the Angiosperms353 dataset was excluded from the genetic analyses.

1.6 Challenges and limitations

The COVID-19 pandemic, while no longer a current public health issue, continues to exert adverse effect to the post-graduate study projects initiated during the public health emergency. This PhD studentship is a cotutelle programme jointly registered at both the University of Montpellier and Universiti Putra Malaysia. The initial project plan

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involved field trips for samplings in Southeast Asia, laboratory analyses in Montpellier, and inter-university travel. Additionally, extensive sampling across the natural distribution of study objects in Southeast Asia is imperative. However, travel restriction imposed due to the pandemic impeded the progress of the project.

The natural distribution of both origin cultigens and wild relatives spans multiple countries in Southeast Asia. Securing collection and export permits from various countries across the region is inherently challenging even under ordinary circumstances, let alone during a global pandemic. The travel restrictions, therefore, presented a challenge to the timely execution of the project.

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