Review

Origin and Domestication of Native Amazonian Crops

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Abstract: Molecular analyses are providing new elements to decipher the origin, domestication and dispersal of native Amazonian crops in an expanding archaeological context. Solid molecular data are available for manioc (*Manihot esculenta*), cacao (*Theobroma cacao*), pineapple (*Ananas comosus*), peach palm (*Bactris gasipaes*) and guaraná (*Paullinia cupana*), while hot peppers (*Capsicum* spp.), inga (*Inga edulis*), Brazil nut (*Bertholletia excelsa*) and cupuassu (*Theobroma grandiflorum*) are being studied. Emergent patterns include the relationships among domestication, antiquity (terminal Pleistocene to early Holocene), origin in the periphery, ample pre-Columbian dispersal and clear phylogeographic population structure for manioc, pineapple, peach palm and, perhaps, *Capsicum* peppers. Cacao represents the special case of an Amazonian species possibly brought into domestication in Mesoamerica, but close scrutiny of molecular data suggests that it may also have some incipiently domesticated populations in Amazonia. Another pattern includes the relationships among species with incipiently domesticated populations or very recently domesticated populations, rapid pre- or post-conquest dispersal and lack of phylogeographic population structure, e.g., Brazil nut, cupuassu and guaraná. These patterns contrast the peripheral origin of most species with domesticated

populations with the subsequent concentration of their genetic resources in the center of the basin, along the major white water rivers where high pre-conquest population densities developed. Additional molecular genetic analyses on these and other species will allow better examination of these processes and will enable us to relate them to other historical ecological patterns in Amazonia.

Keywords: molecular markers; genetic analysis; phylogeography; phylogenetics; crop dispersal

1. Introduction

At least 138 crops with some degree of domestication were being cultivated or managed by native Amazonians in various types of production systems at the time of European conquest, including 83 crops native to Amazonia and immediately adjacent areas in northern South America, and 55 exotic ones, *i.e.*, from other Neotropical regions, such as northeastern Brazil, the Caribbean and Mesoamerica [1]. Among the 52 crops with domesticated populations, 14 are fruit or nut trees or woody vines (27%); among the 41 crops with semi-domesticated populations, 35 are trees or woody vines (87%); and among the 45 crops with incipiently domesticated populations, all but one are fruit and nut trees. Overall, 68% of these Amazonian crops are trees or woody perennials. In landscapes largely characterized by forest, a predominance of tree crops is perhaps not surprising [1]. Nonetheless, the most important subsistence crop domesticated in Amazonia is an herbaceous shrub, manioc [2], and several other domesticates are also root or tuber crops, most of which are adapted to savanna-forest transitional ecotones with pronounced dry seasons.

Two types of domestication can be distinguished conceptually: landscape domestication and plant (or animal) population domestication [1]. Only the latter will be considered here because plant population domestication can now be examined with new genetic techniques, even though both sorts of domestication are of potential interest to historical ecology, since landscapes and the biota in them are profoundly affected, indeed molded by human actions. Additionally, these two kinds of domestication are intimately related because domesticated populations require some kind of landscape management, especially cultivation. Plant population domestication is a co-evolutionary process by which human selection on the phenotypes of promoted, managed or cultivated individual plants results in changes in the descendent population's phenotypes and genotypes that make them more useful to humans and better adapted to human management of the landscape [1]. The degree of change in populations can vary along a continuum from wild (the baseline, with no human-mediated change), through incipiently domesticated, to semi-domesticated, to domesticated. An incipiently domesticated population has gone through a founder event (defined as human selection of a small sample of the wild population and propagation of descendents from this sample; also called a bottleneck) that reduces its genotypic diversity and its phenotypic diversity varies only somewhat from the ancestral wild population in the traits selected by humans. A semi-domesticated population has gone through several sequential founder events that reduce further its genotypic diversity, but its phenotypic diversity is enhanced by accumulation of diverse alleles for traits selected by humans. Semi-domesticated populations tend to

have more ample geographic distributions than incipient domesticates, which may permit introgression with other wild, incipient or semi-domesticated populations of the same species; in turn, such introgression may offer additional alleles for selected traits, thus somewhat enhancing genetic diversity. The ample geographic distribution may include areas where wild populations do not exist, which reduces introgression of wild-type alleles and permits more rapid response to human selection. A domesticated population has been further selected for adaptation to human-modified landscapes, especially cultivated gardens and fields, and has lost its original ecological adaptations for survival without humans, especially its original dispersal mechanisms and survival capabilities [1]. Observe that domestication is a process that occurs at the population level, not the species level, so that it is incorrect to affirm that species X is a domesticate, unless all wild populations have become extinct, which is an uncommon occurrence; it is most generally correct to affirm that species X exhibits domesticated populations. Exceptions to this generalization exist, for example, when the end-result of the domestication process is a new species; a particular case of the latter is interspecific hybridization followed by chromosome doubling, resulting in the formation of allopolyploids [3], as in guaraná, discussed below. An aside is worth adding here: the term "proto-domesticate" is often used, but *protós* is Greek for "first", leading to definitions such as 'original' and 'primitive' (as in "first order"); since domestication is a process and the domesticated population is the result, the domesticate is not primitive, but derived. Hence, the term should be avoided.

The degree of modification during domestication can be dramatic in many crops, including some tree crops, such as peach palm, where the difference in fruit size between the wild type and the most derived domesticated population is on the order of 2000% [4]. Several other Amazonian tree crops show considerable, although not as dramatic, modification due to domestication [5]. Given the long generations and typically outcrossing reproductive systems, these degrees of change suggest that domestication started quite early, perhaps at the beginning of the Holocene, rather than when production systems coalesced and became prominent 3,000 to 4,000 years before present (BP). The archaeological record, however, does not contain early records of Amazonian tree crops, although manioc and sweet potato were present between 8,000 and 6,000 BP in caves along the western Andean foothills of Peru [6], indicating that they were domesticated earlier. The earliest lowland tree crop, guava, was present in the same area before 5,000 BP [6]. The archaeological record of lowland South America east of the Andes is much less studied than the dry Pacific coast, western foothills and the highlands, where preservation is better, but is gradually gaining attention and patterns will become apparent as critical mass increases.

Better ethnographic and historical information exists for more recent periods. The crops in Amazonia at conquest were distributed in numerous centers, regions and micro-centers of crop genetic diversity, located principally where Native Amazonian populations were most abundant [7], *i.e.*, along the principal white water rivers, but also in the upper Negro River, which was and still is a major center of Amazonian ethnic and linguistic diversity. Some tree crops, such as Brazil nut, are quite long-lived (500 to 1,000 years), so that their pre-conquest distribution can be mapped from their modern distribution. Balée [8] used this type of information to estimate the proportion of the Amazon basin that had been modified by pre-conquest human activity (nearly 12%). Unfortunately, few species permit this type of analysis, but living plants can provide other information that permits inferences

about their origin, domestication and dispersal before and since European conquest. This information is in their DNA and is accessed with different molecular techniques.

There are numerous types of molecular markers used in genetic analysis, each with advantages and disadvantages, as well as different information contents [9]. In plants, both nuclear DNA (diploid) and chloroplast DNA (haploid) offer important and somewhat different information, with nuclear DNA subject to rapid change via recombination and chloroplast DNA subject to less rapid change; the latter is generally maternally inherited, which makes it especially useful for some kinds of analyses, such as distinguishing seed dispersal from pollen dispersal. So called dominant markers are cheaply and easily generated, but are less informative because they do not distinguish between homozygotes and heterozygotes at a particular DNA locus; the primary marker cited here is Random Amplified Polymorphic DNA—RAPDs, which are generated principally from nuclear DNA. Co-dominant markers are often more expensive to generate, but are more informative because they distinguish homozygotes and heterozygotes; examples are protein polymorphisms, especially in enzymes, Simple Sequence Repeats—SSRs (also called microsatellites), and Restriction Fragment Length Polymorphisms—RFLPs; the latter two can be either nuclear or chloroplast. Direct sequencing of specific regions of DNA is becoming the most important strategy to study genetic variability as the cost falls continually; it is also the most informative. Sequence polymorphisms include insertions and deletions of base pairs or sections of DNA, as well as substitutions in nucleotide sequences, such as Single Nucleotide Polymorphisms—SNPs. Ideally molecular markers should be selectively neutral, that is they should not be under selective pressures so that they do not reflect different local adaptations to natural or human selection.

New research with these molecular tools attempts to identify origins and possible dispersals via the patterns of genetic diversity in living populations of native Amazonian crops, a field of study known as phylogeography [9]. Phylogeography is the analysis of the geographic distribution of genetic variants, especially lineages of genes, which is generally due to dispersal of organisms (seed dispersal in plants) and thus provides insight into the history of a species. The same information permits inferences about the domestication process [10-12] and can even be used to estimate the approximate age of the founder events, although this has yet to be attempted with an Amazonian crop. This contribution reviews recent molecular studies of a set of native Amazonian crops, some important, others less so, and identifies emergent patterns that can be used to interpret crop domestication and dispersal before conquest.

2. The Crops

We will review the recent molecular genetic literature on only nine of the 83 native Amazonian crops, principally because the number of crops examined is still quite small. Manioc is the most important subsistence food crop domesticated in Amazonia and was one of the first studied with molecular techniques. Cacao is arguably as important, although chocolate lovers might place it first. Peach palm is the premier Neotropical tree fruit-crop and has recently been the focus of considerable research. The *Capsicum* peppers are certainly the most important Neotropical spices and at least one species appears to contain domesticated populations of Amazonian origin. Pineapple is often considered the queen of fruits and is certainly the most important fruit crop from Amazonia. Inga is a legume tree crop often called ice cream bean because of the edible aril around the large seeds; it is

currently an important agroforestry species, used principally for green manure and shade for other crops. Guaraná is a stimulant that is gaining worldwide popularity, although its principal use in Brazil is to flavor soft drinks. Brazil nut is the emblematic Amazonian tree, whose edible seed is recognized around the world. Cupuassu is a cacao relative whose pulp is used for making fruit juices and other products.

Manioc, peach palm, *Capsicum*, pineapple, inga and guaraná all have domesticated populations, while cacao has semi-domesticated populations, and Brazil nut and cupuassu have incipiently domesticated populations [1]. Eight of the nine are outcrossing species, the exception being *Capsicum*, and two are generally vegetatively propagated (manioc and pineapple). The available information concerning these nine species is not uniform, as much remains to be done. Nonetheless, the information now available and reviewed here provides fascinating insights into the origin and domestication of native Amazonian crops, placing Amazonia squarely in the list of important centers of crop genetic diversity.

2.1. Manioc

Manioc (*Manihot esculenta* Crantz, Euphorbiaceae) is the most important food crop that originated in Amazonia and is grown throughout the tropics; it is the sixth major food crop produced globally. The term manioc is derived from the Tupi word *maniot*, while the term cassava comes from the Arawak words *cassavi* or *cazabi*, meaning bread [13]. Although some modern cultivars derive from modern breeding efforts and market demand, manioc is mostly cultivated by traditional farmers with few or no inputs or mechanization. Nonetheless, manioc is extremely important to the food security of an enormous number of smallholders in tropical countries and is the main carbohydrate resource for about 800 million people.

The origin of manioc as a crop has long been debated. The genus *Manihot* has 98 species distributed throughout the Neotropics from Mexico to northern Argentina [14]. Two centers of diversity are recognized: one in Brazil with about 80 species; one in Mexico with 17 species. A taxonomic classification based only on phenotypic variation is unreliable because of considerable trait overlap. For a long time, manioc was considered a cultigen (without a wild conspecific ancestral population) and was thought to have originated from a series of introgression events among wild species [14]. Based on phenotypic similarities, *M. aesculifolia*, which occurs in Mesoamerica, was thought to be one of these wild relatives [14]. Later, another Mesoamerican species, *M. carthaginensis*, was proposed as a wild relative [15,16]. Early studies with molecular markers did not clearly resolve the phylogeny of the genus [17,18]. However, they did identify a clear separation between the Mesoamerican and South American lineages, and found that cultivated manioc always grouped with South American species, suggesting that the crop was domesticated in South America. The great phenotypic variation and the low-resolution phylogenies also suggest that the genus *Manihot* experienced a recent period of super-diversification.

The taxonomy of *Manihot* was elucidated in the mid-1990s. Based on phenotypic traits, Allem [19] proposed that manioc consists of three subspecies: *Manihot esculenta* ssp. *esculenta* (cultivated form), *M. esculenta* ssp. *flabellifolia* (the closest wild relative) and *M. esculenta* ssp. *peruviana* (probably not involved in manioc domestication). Together with *Manihot pruinosa*, these form the primary gene pool

of manioc. Allem also speculated that manioc was domesticated somewhere on the Central Brazilian Plateau, the main center of diversity in South America, where 53 *Manihot* species occur.

Three different molecular markers [sequencing of the nuclear gene glyceraldehyde 3-phosphate dehydrogenese (G3*pdh*), SNPs and SSRs] were used to evaluate the relationships among cultivated varieties of manioc and wild populations of *M. esculenta* ssp. *flabellifolia* and *M. pruinosa*. It was determined that the latter species does not contribute to the gene pool of cultivated manioc and that the genetic variability found in cultivated manioc is a subset of the genetic variability found in the populations of *M. esculenta* ssp. *flabellifolia* that occur in southwestern Amazonia [2,20,21]. Recently Léotard *et al*. [22] used the G3*pdh* gene to examine cultivated manioc, a wider geographic sample of *M. esculenta* ssp. *flabellifolia* and other potentially hybridizing *Manihot* species, and validated Olsen and Schaal's results [2,20,21], strongly suggesting that manioc was domesticated only once from *M. esculenta* ssp. *flabellifolia* populations occurring in northern Mato Grosso, Rondônia and Acre states, in Brazil, and adjacent areas of northern Bolivia. Domestication must have started before 8,000 BP, as that is the earliest date reported from the Zana and Ñanchoc valleys of coastal Peru [6].

The domestication of manioc resulted in significant changes in *M. esculenta* ssp. *flabellifolia*, the most important being the development of tuber roots capable of storing large amounts of carbohydrates. After its initial domestication, different selective pressures gave rise to two major groups of varieties: "sweet" manioc and "bitter" manioc [23,24]. This separation is based on the cyanogenic potential of the roots, which accumulate linamarin and lotaustralin, substances that are hydrolyzed to cyanide when the root cortex tissues are damaged. Sweet varieties have low amounts of cyanogenic glycosides (<50 ppm fresh weight) and can be safely consumed with simple processing (cooking or sometimes even raw). On the other hand, bitter varieties have large amounts of cyanogenic glycosides (>50 ppm fresh weight) and demand considerable detoxification and processing before consumption in the form of flour (*farinha*, *farine*), flat breads (*beiju*), cassava bread or fermented drinks. Although this classification is dichotomist, continuous variation among manioc varieties and related wild species is observed, suggesting that sweet and bitter manioc are the outcome of independent selections from an ancestor with intermediate toxicity [25].

In contrast to what is observed in most domesticated crops, there is strong selection for manioc varieties with high toxicity, especially in Amazonia where the majority of varieties are bitter. Some studies identify a tendency for higher yield in bitter varieties than in sweet ones, which may be due to the greater pest and pathogen resistance of bitter manioc varieties [26,27]. In Tukanoan settlements in northwestern Amazonia the selection of varieties appears to be due mainly to the foods that can be prepared from them and bitter manioc can be used to prepare more kinds of food [28].

In general, bitter manioc cultivation is associated with the courses of the major Amazonian rivers, as well as the coastal areas of South America, where population densities were highest before conquest. On the other hand, sweet manioc is the main crop throughout the headwaters of these same rivers in western Amazonia, including the whole length of the Ucayali and Marañon Rivers in Peru, the southern periphery and up into Mesoamerica. It is also commonly grown on a minor scale where bitter manioc is the major crop [25]. These patterns may be due to the costs and benefits of toxicity, with greater benefits of toxicity for large sedentary populations with semi-permanent fields, because these attract greater pest and pathogen pressure, and with greater costs for small, more mobile

populations [25]. While these ideas may explain pre-conquest distributions, it is not clear if they explain current distributions of bitter and sweet.

Although ease of vegetative propagation is another outcome of domestication, manioc has not lost its capacity for sexual reproduction, which plays a very important role in the evolutionary dynamics of the crop. Once produced, seeds become part of the soil seed bank, and seedlings sprout among the vegetatively propagated varieties in the plots [25,29-31]. Many smallholders let these volunteers grow, either unconsciously or consciously [32,33]. At the time of harvest, they decide if a given volunteer is worth including among the plants that will be vegetatively propagated [25,32,34,35]. If so, smallholders can either incorporate the seedlings into an existing variety or use them to establish a new variety [25,29,31,36,37]. Genetic analyses confirmed seedling incorporation by detecting high polymorphism in local varieties [24,31,36,38], and by demonstrating that local varieties are polyclonal, with one predominant clone and a set of morphologically similar plants that are genetically different [30,34,39].

2.2. Cacao

Cacao (*Theobroma cacao* L., Malvaceae) is native to Amazonia, but is generally believed to have been domesticated in Mesoamerica [40], since this is the only region in which evidence of cultivation existed at the time of European conquest [41]. The name *Theobroma,* or "food of the gods," was coined by Linnaeus to honor the Aztecan belief in the divine origin of cacao, although he might not have chosen it if he had experimented with the Aztecan beverage made with a mixture of fermented and ground cacao seeds, maize and *Capsicum* peppers. The specific name *cacao* and the term *chocolate* are corruptions from Nahuatl, the Aztec language. The chocolate that we are all familiar with is a European invention, made with vanilla and sugar, and much easier to accept as a "food of the gods" than that made with maize and chili peppers. Although the Maya have been credited with its domestication, the name for cacao can be reconstructed in proto-Zapotecan, a language spoken in southern Mexico by about 3,350 BP, while proto-Mayan is dated to about 2,400 BP [42], strongly supporting a much earlier dispersal.

Until recently there were three hypotheses about the relationships among cultivated cacao in Mesoamerica and wild cacao in Amazonia [40]: a south to north dispersal; a north to south dispersal; and *in situ* development of types with no early dispersal. These hypotheses attempt to explain the differences between the Criollo types (subsp. *cacao*; [43]) found from northwestern South America to Mesoamerica and the Forastero types (subsp. *sphaerocarpum*) found in Amazonia and northeastern South America, while accepting the observation that cacao grows wild from southern Mexico to the southern edges of Amazonia. However, cacao survives easily in appropriate humid forest ecosystems when abandoned, which led Clement [1] to classify it as a crop with semi-domesticated populations, rather than with fully domesticated populations.

Using two co-dominant markers (RFLPs and SSRs), and controlling sample origin very carefully to distinguish between materials that were less likely to have been genetically contaminated by the last five centuries of germplasm exchange, Motamayor & Lanaud [44] show clearly that Criollo types are derived from South America, as had been hypothesized by Cheesman [45], who identified the center of origin in the upper Napo, Putumayo and Caquetá River basins adjacent to the Ecuadorian and

Colombian Andes. Motamayor and Lanaud suggest that northwestern Venezuela may be important because there are very early reports of a chocolate-like beverage called *chorote*, religious use and extraction of seed fat all based on genetically Criollo type cacao. These early reports should be interpreted with caution, however, as they may already reflect European influences [41], rather than purely native developments, and no archaeological records of cacao exist in the region [44]. There are also no reports of cultivation in this area until much later [41].

One of the major implications of this study is that Cuatrecasas' [43] classification of two subspecies is incorrect [44], which also raises questions about the usefulness of the Criollo-Forastero dichotomy, even though numerous molecular genetic analyses have identified clear differences between these types (references in [44,46]). These conclusions led to a search for a new intraspecific classification that would be useful for plant breeders [46]. With a very large data set (1,241 plants; 96 SSR), the Structure program [47] was used to identify genetic groups with no *a priori* hypotheses, which also allowed identification of genebank errors and their elimination [46].

Instead of the two traditional groups (Criollo and Forastero) and their hybrid (Trinitario), ten genetically different clusters are strongly supported by Structure and various other analyses [46]. The greatest diversity is found in western Amazonia (7 groups, including Nacional). Three groups are especially important to our discussion: Criollo, Nacional and Amelonado. These groups have been classified as traditional cultivars [46], which suggests some degree of domestication. The Criollo traditional cultivar is found in northwestern Ecuador, northwestern Venezuela (around Maracaibo), northern and western Colombia, and throughout Central America to southern Mexico, including the Maya heartland. The Nacional is a western Ecuadorian cultivar, with close affinity to several populations in extreme northern Amazonian Peru and the Curaray group in Amazonian Ecuador. The Criollo, Nacional and Curaray groups occupy one major branch of the Neighbor Joining dendrogram, suggesting an Ecuadorian Amazonian origin for both traditional cultivars. The Amelonado occurs in the lower Amazon basin and has less morphological variation than other Amazonian cacaos, especially with respect to fruit characteristics [40]. The Amelonado groups with the French Guiana group, suggesting a possible eastern Amazonian origin for this traditional cultivar. Close scrutiny of the molecular information shows that these three traditional cultivars have low numbers of private alleles (alleles that occur in only one group), while the western Amazonian groups generally have high numbers, with one or two exceptions that may be due to sampling [46]. One way to explain these low numbers is that they represent the genetic bottlenecks that accompany continued selection by humans, which is never doubted for Criollos.

Note also that the Criollo and Amelonado traditional cultivars are at the northwestern and eastern extremes of cacao distribution in the Americas. The discussion of Criollos has always included human-mediated dispersal, although clear records of cultivation appear only in the northern half of its range, from Costa Rica to Mexico [41]. The early chronicles from eastern Amazonia do not report cultivation. However, Patiño [41] cites Jacques Huber [48], who refers to the lack of cacao east of Obidos and Santarén and west of Marajó Island. Patiño [41, p. 351] concludes that the cacao in eastern Pará is probably the result of "ancient cultivation." Ethnographic observations in French Guiana also suggest that cacao has long been cultivated in the region by native peoples [49]. While both Huber's and Barrau's observations are much too late to offer assurance that cacao was cultivated before conquest, the relative uniformity of Amelonado fruits and the low number of private alleles

suggest that this traditional cultivar may have been at least incipiently domesticated in eastern Amazonia.

It is appropriate to ask why only Criollos are generally considered to be at least semi-domesticated, whereas even the traditional cultivars Nacional and Amelonado are not. It may be that cacao researchers have been blinded by the name "food of the gods." In other words, if Native Americans did not make chocolate, then they did not domesticate cacao. Considering that numerous other Amazonian fruits with sweet juicy pulps contain domesticated populations [1], such as abiu (*Pouteria caimito*), biribá (*Rollinia mucosa*), mapati (*Pourouma cecropiifolia*), sapota (*Quararibea cordata*), it is possible that cacao could have been selected initially for its pulp. In fact, this is probably the only way to get cacao from Amazonian Ecuador (the Curaray group) over the Andes into western Ecuador (the Nacional traditional cultivar), then up the Colombian Pacific and around to Maracaibo, before or simultaneously going north into Panama and Costa Rica. Remember that there were no reports of cultivation in any of these areas, nor any reports of chocolate, except the *chorote* in northwestern Venezuela.

Any sweet fruit can be fermented to obtain a mildly alcoholic beverage. Recent chemical archaeology shows that several types of pottery vessels found in Honduras, part of the Mayan heart-land, contain theobromine, a chemical compound found in *Theobroma* spp. The earlier vessels have shapes that suggest they were used to serve a fermented beverage, while the later vessels have shapes characteristic of those used with frothed chocolate [50]. Interestingly, the earlier vessels date to 3500 BP, in close agreement with the appearance of the word for cacao in proto-Zapotecan by 3350 BP [42]. The authors suggest that the first uses for cacao in Mesoamerica were similar to those in South America—the sweet pulp around the seed was consumed directly or fermented—and only later did the fermented seed itself become an additional part of the beverage, finally becoming the "food of the gods." While there are no reports of the cacao pulp beverage in South America, numerous other fermented beverages made from sweet or starchy fruits and roots are mentioned [41].

For domestication to occur, there must be human selection and propagation, both of which can be either intentional or unconscious [1,51]. Most domestication events were surely initially unconscious and cacao is an ideal example of how this might have occurred. Some variation in fruit pulp sweetness and juiciness exists in any natural cacao population, and humans who collected cacao to suck on the pulp would soon learn which trees offered the best fruit. These trees would be preferred for harvesting a sack of fruit to take back to camp or along a trek into another river basin. At camp, discarded seeds would germinate immediately and grow to reproductive age if environmental conditions were appropriate; if they germinated and grew in dump heaps they would even be less dependent on environmental conditions because of extra nutrients and light [52]. These new populations around camps would be more homogeneous than the source populations, but would certainly contain progenies from numerous seed trees, allowing for crossing among selected types, which in turn would yield sweeter and juicier pulps in the next generation. If this occurred in Amazonian Ecuador or in French Guiana, cacao could be rapidly dispersed over the Andes or into the estuary of the Amazon River, respectively, without any cultivation, but with selection and propagation. Further genetic analysis can certainly shed more light on this hypothesis.

2.3. Peach Palm

The peach palm (*Bactris gasipaes* Kunth, Arecaceae) is the only Neotropical palm with domesticated populations [4]. It may have been selected initially for its wood, preferred for tool making, and later for its abundant oily fruits, and finally for starchiness in the fruits, making them good for fermentation [53]. Peach palm is currently an agribusiness for its hearts-of-palm. The species presents considerable morphological and genetic variability in its wild and cultivated populations, due to adaptation to different environments and different stages of domestication, respectively. Thousands of years of domestication have resulted in landraces, each of which has common morphological, chemical and productive characteristics due to a common genetic origin [54]. These landraces are widely distributed in the humid Neotropics, especially Amazonia.

Throughout the 20th century, peach palm was considered a cultigen, with no wild conspecific ancestor. The revision of *Bactris* [55] gathered all cultivated populations of peach palm into var. *gasipaes* and all wild populations (previously identified as species) into var. *chichagui* (H. Karsten) Henderson. Within var. *chichagui* three types were proposed, with little description of their fruits and without detailing their distributions, which was done later by others [56] (Figure 1). Nonetheless, this revision now permits phylogenetic hypotheses that can be tested with genetic tools.

Figure 1. Distribution of the three wild types of *Bactris gasiapes* var. *chichagui* [56].
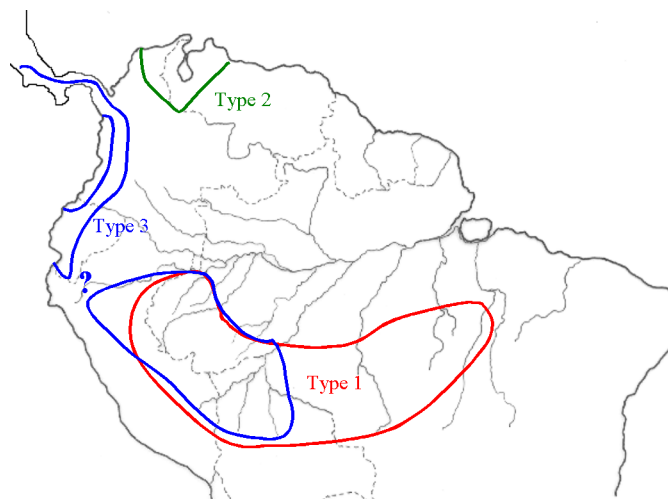
There is considerable speculation about the origin of the founder event(s) that lead to domesticated peach palm populations, with three hypotheses currently under consideration: (1) a single domestication event in southwestern Amazonia [57], with some morphological [58] and molecular (RAPDs, a dominant marker; [59]) evidence, and the occurrence of two wild types (1,3); (2) a single domestication event in northwestern South America, with archaeological coincidences [60] and the occurrence of a wild type (3); and (3) multiple domestication events in the distribution of two wild types (1,3), with coincidences in common SSR allele frequencies between var. *chichagui* and var. *gasipaes* in some localities [61,62]. Determining the correct hypothesis will require analysis of the landrace complex and its relationships with the various populations of the three wild types, a complex task given introgression between domesticated and wild populations [63].

Some of the landraces have been characterized morphologically and mapped [64]. The identification and classification of Amazonian landraces was based on morphometric characterization and multivariate analyses using a descriptor list designed for *in situ* and *ex situ* use. A hierarchical classification based on fruit size was proposed [64], with microcarpa landraces having small fruit (<20 g; Pará, Juruá and Tembe), mesocarpa landraces having intermediate sized fruits (20–70 g; Pampa Hermosa, Tigre, Pastaza, Solimões, Inirida, Cauca, Tuira, Utilis, Guatuso and Rama), and macrocarpa landraces having large fruits (>70 g; Putumayo and Vaupés) (Figure 2). The size of the fruit reflects the degree of modification due to human selection during the domestication of peach palm [57].

Figure 2. Geographical distribution of landraces of *Bactris gasipaes* var. *gasipaes*: 1. Rama, 2. Utilis (including Guatuso and Tuira), 3. Cauca, 4. Tembé, 5. Juruá, 6. Pará, 7. Pampa Hermosa, 8. Tigre, 9. Pastaza, 10. Inirida, 11. Putumayo (including Solimões), 12. Vaupés [after Rodrigues *et al*. [59], with modifications].
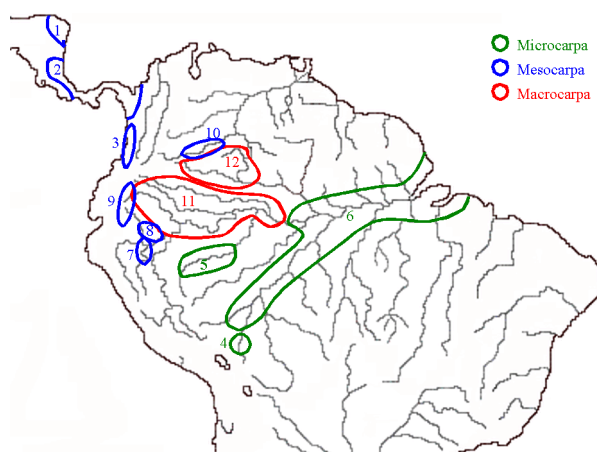
Several genetic studies have been conducted over the last decade to understand the great genetic variability within and among landraces. The first study used isoenzymes (co-dominant markers) and found that the Pará landrace of eastern Amazonia grouped with the Tembé population of northern Bolivia (once designated *Guilielma insignis* Martius [55]), while the other landraces grouped on another branch of the dendrogram [65]. The authors proposed geneflow along the Madeira River to account for this grouping, as well as geneflow through western Amazonia to Central America.

Dominant RAPD markers have been used extensively by the Brazilian group to validate many of the landraces in the genebank. One study concluded that the Pará, Putumayo, Pampa Hermosa and Utilis landraces are valid, while there is only one landrace in Central America rather than three and the Solimões landrace is part of the Putumayo landrace in western Amazonia [59]. This study also observed that the Utilis landrace had lower polymorphism and heterozygosity than the Amazonian landraces. The dendrogram using Nei's [66] genetic distances grouped the Pará landrace with a sample of var. *chichagui* type 1 from Acre, Brazil, and the Putumayo, Pampa Hermosa and Utilis landraces, with a sample of var. *chichagui* type 3 from western Amazonas, Brazil, in the other group. Their dendrogram was very similar to that of Rojas Vargas *et al*. [65], although with more landraces and populations. They proposed the most parsimonious hypothesis: a single domestication event in southwestern Amazonia, with two dispersals, one to the northeast and another to the northwest. A

second study used the same RAPD markers, the same landraces, as well as samples of the Juruá, Cauca and Vaupés landraces, and samples of var. *chichagui* type 1 from the Xingu River, Brazil, and type 2 from the Magdalena River, Colombia [67]. This study confirmed the previous validation [59] and the separation of the Pará landrace from the others, as well as validating the Juruá landrace and eliminating the two wild populations as parents of domestication events. A third study with the same markers, landraces and additional populations [68] revalidated the landrace complex, confirmed the Pará landrace as having affinities with the upper Madeira River, and further confirmed the Western Amazonian complex as separate from the southeastern complex. The third study also designed a core collection within the Brazilian genebank to stimulate further morphological characterization, permit duplication and facilitate future analysis of the phylogeography and phylogenetics of *Bactris gasipaes*.

During the last decade, numerous microsatellite primers were developed and tested [69-71]. Four of the first set were used to examine relationships among seven wild and eleven cultivated populations [62]. They detected considerable introgression among adjacent wild and cultivated populations, as expected following the study in Ecuador [63]. Unfortunately, they did not analyze the cultivated and wild populations separately, and created a Neighbor Joining dendrogram from Nei's minimum genetic distance, which they interpreted as showing three domestication events, even though the dendrogram's topology was not much different from the first RAPD study [59]. They also excluded the Pampa Hermosa landrace from the final dendrogram, although it was part of their preliminary study [72], which found a topology even more similar to the first RAPD study. Although quite intriguing, the small number of microsatellites does not permit much precision.

After a decade of study, the origin of the cultivated peach palm is still speculative, principally because of the numbers and types of markers used. A new study [73] with 17 microsatellite loci examined the phylogeography of the landrace complex represented in the newly created core collection [68], which has 40 accessions. This phylogeographic analysis used the Structure program to revalidate landraces and Nei's [66] genetic distance to create a Neighbor Joining dendrogram, which was quite similar to the first and subsequent RAPD dendrograms [59,67,68], as well as the first microsatellite dendrogram [72]. Relationships with two var. *chichagui* types suggest considerable introgression.

Universal chloroplast DNA sequences [74] are now being used to determine the phylogenetic relationships among cultivated and wild populations in the core collection, as well as the closely related *B. riparia* and the more distantly related *B. simplicifrons*, both used as outgroups. Because the chloroplast genome is generally maternally inherited, these sequences should identify one or a few haplotypes within the landrace complex, one or two of which may also occur in var. *chichagui*, which would pinpoint the wild populations involved in the domestication of the landraces, as was done with manioc [20]. The first results using these cpDNA sequences showed that one of the cultivated landraces, Pará, has chloroplast haplotypes different from the other cultivated and wild populations (Cristo-Araújo *et al.*, Unpublished), suggesting that peach palm was domesticated more than once, as hypothesized by Mora Urpí [61], although southwestern Amazonia still seems to be the primary region of origin, as hypothesized by Rodrigues *et al.* [59].

2.4. Capsicum Peppers

The genus *Capsicum* (Solanaceae) undoubtedly originated in the Americas [75], although one species is named *C. chinense*, suggesting an Asian origin; in fact, *C. chinense* is the most Amazonian of the *Capsicum* peppers [76,77]. The earliest record of pepper use is from archaeological excavations in the Valley of Tehuacán, Mexico, and date from about 8,500 BP [78]. Starch derived from chili peppers and preserved on artifacts from seven archaeological sites ranging from the Bahamas to Andean South America appeared by 6,000 BP [79]. The peppers were present from the north of Chile and Argentina to northern Mexico and the southern United States at the time of European conquest [76,77]. Today they are distributed worldwide and grown for use as spices, vegetables, ornamental plants and medicine, in temperate and tropical areas [76].

Several criteria are used to determine more precisely where a domesticated population originated and in which directions it was dispersed: The crop must have been domesticated somewhere in the range of its wild relatives, the center of diversity may indicate the center of domestication of the crop, and archaeological, historical and linguistic data can provide evidence [80,81]. The prehistoric dispersals of wild peppers were probably due to birds before humans became important dispersal agents [82]. Different species of *Capsicum* were domesticated independently in several regions of the Americas [10,83]. Three regions are considered to have been independent areas of *Capsicum* domestication: Mesoamerica, the Andean region and the tropical lowlands of South America [10]. In each area of origin, one or more species was brought into domestication, perhaps intentionally, perhaps not, and they were then dispersed to different areas where they continued to be selected, resulting in distinct morphological types. Domestication resulted in changes, especially in the fruits. The fruits of the wild types are small, erect, red and deciduous, while fruits of domesticates are larger, often pendent, not deciduous and varied in color. Domestication also resulted in changes in reproduction and the level of pungency [76,77,83,84].

Currently, *Capsicum* includes about 25 wild species and 5 species with domesticated populations: *Capsicum annuum, C. frutescens, C. chinense, C. baccatum* and *C. pubescens*. The *C. annuum-chinense-frutescens* complex may have arisen from a widely distributed complex of closely related wild and weedy species [85]. In an attempt to resolve this question, the chloroplast *atpB-rbcL* noncoding spacer region was used to examine the phylogeny of *Capsicum*, using 11 *Capsicum* species and seven outgroups [86]. The *annuum* group consists of *C. annuum, C. chinense, C. frutescens*, and *C. galapagoense*, without clear morphological unity but with strong support from isozymes. Only the wild progenitor of *C. annuum* is known: *C. annuum* var. *aviculare*. Without identification of the wild progenitor, identification of the center of origin of a domesticated population is extremely difficult [80].

The center of diversity of *Capsicum* is in South America, with most species in Brazil and Bolivia. Studies in cytogenetics, molecular genetics, archaeology and biogeography established probable centers of origin of each domesticated species [80]. The center of origin of the economically most important *C. annuum* (chili, jalapeño, cayenne) is in Mesoamerica, more precisely in upland central-eastern Mexico [87], confirmed by molecular analysis. The centers of origin of the other domesticated lowland species are not yet clear, but it is believed that Amazonia is the center for *C. chinense* (cumari, murupi, habanero, biquinho), where its variability is greatest, and Amazonia may be

the center for *C. frutescens* (cayenne, tabasco) [78], although Mesoamerica is also a candidate given abundant morphological diversity [10]. Remains of a reputed *C. chinense* were found at Guitarrero Cave, in the western Andean foothills of northern Peru and dated as earlier than 9000 BP, while *C. frutescens* only appears in the same region (Huaca Prieta) at about 3,500 BP [6]. Recently, an apparently wild sample of *C. chinense* was found in Roraima, Brazil [88], offering the possibility of a more precise origin for this species, but a wild population of *C. frutescens* has not yet been found in Amazonia or Mesoamerica. Subsequently, both species were distributed from the Amazonian lowlands to southeastern Brazil, Central America and the West Indies [76,89], but the famous habanero arrived in Mexico only after the conquest, which explains its name, as Habana is the current capital of Cuba, where the Taíno people, of the Arawakan language family, had introduced it before European conquest. Southwestern Amazonia, more precisely the lower Andean valleys of Bolivia, is considered the center of origin for *C. baccatum* (girl's finger, chili or ají) and its distribution was less extensive before European conquest [9,82,89]. The earliest archaeological remains of *C. baccatum* are from Huaca Prieta and Punta Grande, in the western Andean foothills of Peru, dated to before 4,000 BP [6].

2.5. Pineapple

At the time of European conquest, the pineapple (*Ananas comosus* var. *comosus* (L.) Merr., Bromeliaceae) was cultivated in all the Neotropical lowlands, from Mesoamerica and the Antilles southward to Paraguay and the humid valleys along the Pacific coast of Peru, and specific cultivars had been developed for the Andean hillsides, where they are still important in Colombia, Venezuela and Peru. Its Latin name is derived from the word *nana* and its derivatives, such as *nanas*, *ananas*, or *nanaí* which are widely distributed in most languages of South America and the Antilles. Europeans first learned of this fruit when Columbus arrived on the island of Guadeloupe in 1493. By the end of the 16th century the pineapple was pantropical and its development as a first-rank world fruit crop has been based on pre-Conquest Native American cultivars [90,91].

Wild forms of *A. comosus* are found in all the Neotropical lowlands east of the Andes, from the northern shores of South America to southern Brazil and Paraguay, with the exception of the floodplains of the Amazon and Solimões Rivers and their southern tributaries, where seasonal floods limit natural dispersal [90,92]. More morphological, physiological and genetic variation is observed north of the Amazon River, with two wild botanical varieties, *A. comosus* var. *parguazensis* and *A. comosus* var. *ananassoides*, while only the latter occurs south of the Amazon. *A. comosus* var. *parguazensis* is distributed in the basins of the Orinoco River (the variety name derives from the Parguaza tributary) and the upper Negro River. Similar morphotypes occur in the Guianas, but they developed from a different genetic background [93]. Compared to var. *ananassoides*, var. *parguazensis* is restricted to more humid and shadier habitats, due to its lower water use efficiency [94]. *A. comosus* var. *ananassoides* prefers xerophytic edaphoclimatic conditions, thriving on sand dunes and campinas, rocks and inselbergs, although it may also be found in denser forest. North of the Amazon, it displays much greater morphological and genetic variation than in the south. In particular, many northern clones exhibit appreciable growth of the syncarp after anthesis, resulting in larger and fleshier fruit, while south of the Amazon the fruits are always small and very fibrous, and

the plants show ecological specialization, being restricted to open dry habitats, from arid savannahs to cerrados [94,95].

The distribution of morphological diversity within *A. comosus* suggests that the species originated in the north [96]. The south is the region of origin of another species, the *yvira* or *nana ca çaba* (*A. macrodontes* Morren), not found in the north. This tetraploid lacks a fruit crown and reproduces vegetatively by stolons, forming relatively large stands. Its habitat is the understorey of the humid Atlantic Forest of coastal Brazil and the Parana-Paraguay drainage in southern Brazil, Paraguay and northern Argentina. It was exploited for fiber by the natives [97], but shows no sign of domestication.

Based on a revision of morphological [95], biochemical [98] and genetic diversity [99], Coppens d'Eeckenbrugge *et al*. [90] and Coppens d'Eeckenbrugge and Leal [100] proposed that the north, and more specifically the Guiana shield, is also where the pineapple was domesticated. Coppens d'Eeckenbrugge and Duval [92] refined this hypothesis to take into account recent data on chloroplast DNA variation [93]. The eastern part of the Guiana shield contains considerable phenotypic and genetic diversity, including wild phenotypes with relatively large and fleshy fruits that would have attracted foragers, primitive cultivars and a wide range of large-fruited cultivars. The practice of picking clones in the wild and transferring them to home gardens is still common in eastern Guiana, and many primitive cultivars can survive under secondary forest canopy. This long-term exchange between wild and cultivated populations is confirmed by genetic studies: all four chloroplast haplotypes identified in cultivated materials are present in the wild var. *ananassoides*, supporting the hypothesis that the domesticated var. *comosus* was derived from var. *ananassoides* through selection among those clones with markedly larger syncarps [93].

The domestication syndrome shows both human selection and correlated responses. Greater fruit size resulted from selection for larger individual fruits (pineapple "eyes") and an increase in their number, which also changed their phyllotaxy. A larger number of wider, and generally shorter, leaves provide energy, and a stouter and longer stem allows greater starch storage capacity during the vegetative phase. The latter has been extended by reduced susceptibility to natural flowering induction. Seed production has been reduced through the combination of lower sexual fertility and stronger self-incompatibility [101].

Coppens d'Eeckenbrugge and Duval [92] proposed that var. *comosus* diversified dramatically in western Amazonia, especially in the northwestern center of crop diversity [1] and along the lower Negro River; in both areas a great diversity of advanced cultivars was developed in the absence of wild forms [95]. The peoples of western Amazonia demonstrated brilliant horticultural and plant-breeding skills, as this region is also an important center of domestication and diversification for many other fruits [1,5]. There, pineapple is still a major fruit crop for peoples like the Tikunas [95] and the Huitotos [102], who maintain a wide diversity of cultivars, and it ranks among the primary culturally defined keystone species for peoples like the Letuama. This type of keystone species is one whose existence and symbolic value are essential to the stability of a cultural group over time [103].

The widespread distribution of the pineapple in the Americas at the time of the European conquest, the diversity and quality of the cultivars, not surpassed after one century of modern, intensive breeding, the diversity of uses, the economic and cultural importance of the crop, all point to a very ancient domestication. However, archaeological findings are rather late: 3,200 to 2,800 BP in the valleys of the arid Peruvian Coast [6]; and 2,200 to 1,300 BP from the Tehuac án Valley caves

(Mexico) [104]. The glottochronology of pineapple in Ancient Mesoamerica suggests that the crop was significant by 2,500 BP [42]. Thus, domesticated pineapple was traded and adopted as an important fruit crop on a continental scale more than 3,000 BP. Given the rarity of sexual reproduction in *A. comosus* var. *comosus*, the development of tradable cultivars was necessarily a long and slow process, certainly counted in millennia. Thus, a likely time frame for the divergence between wild and cultivated pineapple lies between 6,000 and 10,000 BP.

Other domestication processes must be considered in *A. comosus*, as there are two other cultivated botanical varieties in the species. The most important is the *curagua* (*A. comosus* var. *erectifolius* [L.B. Smith] Coppens and Leal) developed as a fiber crop via selection from *A. comosus* var. *ananassoides*. It was commonly cultivated north of the Amazon and Solimões rivers, as well as in the Antilles in pre-Columbian times. Its characteristic dense, erect and smooth foliage are the likely result of selection for an abundance of long easily-extractable fibers. Genetic affinity of the curagua with different lineages of var. *ananassoides* indicates multiple and independent domestication events [93,99]. Their antiquity is probably variable, as some clones have reduced fruit production, while others are remarkably fertile.

The domestication process for *A. comosus* var. *bracteatus*, also cultivated for its fiber in Paraguay [97], may have simply consisted of the direct vegetative propagation of rare interspecific hybrids, as this botanical variety has very limited variability. It is native to southern South America and shares nuclear markers with the yvira, indicating ancestral interspecific introgression with this species. Furthermore, the chloroplast haplotype of the rarest form is very similar to that of *A. macrodontes* [93].

The genus *Ananas* is ideal for domestication studies, with multiple processes in time and space, and specialization related to the major uses as a food or as a source of fibers. Selection for fruit characteristics took place where the diversity and quality of spontaneous materials allowed it. The fruit quality induced the crop's dispersal, which in turn induced further diversification and environmental specialization. The development of extremely derived cultivars, in terms of both fruit size and quality, and more particularly the secondary diversification in western Amazonia, despite the lower fertility of advanced cultivars, inevitably raises the question of the capacity of native breeders to exploit sexual recombination, because germination is not easy and seedlings are fragile and grow slowly. The pattern is different for the production of fiber. The domestication process, involving fewer morphological changes, was probably more straightforward for curagua, and could be repeated more easily in time and space, on different lineages of the wild forms. The curagua was widely dispersed, although not so widely as the fruit cultivars, possibly because curagua is not transported/exchanged unintentionally with its propagules, while fruits travel with their crown, and because of competition among domesticated lineages, especially south of the Amazon where large wild stands of *A. macrodontes* or subspontaneous stands of *A. comosus* var. *bracteatus* offered more economical sources.

2.6. Inga

The genus *Inga* includes around 300 species throughout the Neotropics [105] and a history of use by American peoples for at least eight thousand years, mainly for their edible fruits [106]. In Amazonia, *Inga edulis* Mart. (hereafter simply inga) is certainly most important. This is a diploid

legume, predominantly outcrossing and pollinated by small birds, flying insects and bats [107]. It is cultivated for its fruits and wood in indigenous and traditional communities throughout Amazonia, and is considered a priority in many communities of Peruvian Amazonia [108-110]. The history of cultivation of this species is not registered, but morphological studies show that humans have selected inga for a considerable period of time, creating several semi-domesticated populations [1,5,105]. Trees planted in the Peruvian Amazon bear some of the largest pods observed anywhere, and pods under cultivation are much longer and thicker than those in wild populations [105]. Due to these traits, inga has become a model species to evaluate the efficiency of agroforestry systems for the maintenance of genetic resources, as well as for identifying possible origins and bottlenecks associated with domestication.

Hollingsworth *et al*. [111] used five SSR loci to evaluate the maintenance of the genetic diversity in five planted and five natural populations in the Peruvian Amazon. They found less variation in the planted populations compared with the natural [mean corrected allelic richness of 31.3 (planted) and 39.3 (natural), p = 0,009], exactly what is expected in domesticated plant populations [112]. Although lower levels of allelic variation occur in planted populations than in the natural populations, the former still contain on average 80% of the existing allelic diversity found in wild populations. The mean values of expected heterozygosity (0.65 planted *versus* 0.67 natural) indicate that they have not experienced extreme bottlenecks, possibly due to high tree density and the size of the planted populations, and the contribution of pollen and seeds of adjacent plantations and neighboring wild populations.

Nuclear SSRs and chloroplast DNA were used to evaluate the origin of five pairs of planted and wild populations in the Peruvian Amazon, with the intention of determining whether these were derived from local wild populations [113]. The cultivated populations did not have local origin. Nuclear and chloroplast diversity were lower in the planted populations, ~80% and ~70% of the natural populations, respectively, similar to the earlier study [111].

The genetic analyses confirm that inga has domesticated populations, although they do not confirm its degree of domestication, which was suggested to be semi-domesticated [1]. A broad phylogeographic study is needed to understand inga domestication better and to identify the probable origin of the domesticated populations.

2.7. Guaraná

Guaraná (*Paullinia cupana* Kunth var. *sorbilis* [Mart.] Ducke, Sapindaceae) was domesticated in the region between the lower Tapajós and lower Madeira Rivers in Central Brazilian Amazonia by the Sateré-Maué, a people of the Tupi language stock [114]. The first European to mention guaraná was the Jesuit João Felipe Bettendorff [115] in 1669, who observed that the Sateré-Maué were the original cultivators of the vine; he did not mention any other ethnic groups cultivating guaraná The Mundurucu, another Tupi language group, occupy the area immediately south of the Sateré-Maué and do not cultivate guaraná traditionally [116]. Guaraná is important in Sateré-Maué mythology because of its relation with their origin.

As recounted by the Sateré-Maué to the Brazilian ethnographer Nunes Pereira [117] in 1939, the genesis of guaraná involves rivalries between two brothers and their sister, Onhiamuaçabê. The

brothers did not want anyone to marry their sister because she knew all the plants, and which of them were good for curing. She was also the owner of an enchanted place called Noçoquem, where she had planted a Brazil nut tree. One day, a small snake took a fancy to her, so he released a perfume along a trail used by Onhiamuaçabê. She liked the scent a lot. So the snake went further up the trail and touched her lightly on the leg as she passed by. She was immobilized so the snake took advantage of her and she was impregnated. The brothers were furious.

Onhiamuaçabê gave birth to a beautiful boy, and when the boy was old enough, she took him to the enchanted place to eat Brazil nuts. An agouti noticed someone had made a fire at the base of the Brazil nut tree to roast nuts and he reported what he had seen to the brothers. They had guards posted at the enchanted place, and when the boy came the next day to eat some more nuts they decapitated him. His mother heard his cries of anguish, but it was too late. By the time she reached the enchanted place, he was dead. She plucked out the boy's left eye and planted it. But the plant that germinated was no good; it was false guaraná. She then plucked out the right eye and planted it; this grew into true guaraná. She spoke out aloud, as if the child was still alive: "You, my son, will be the greatest force of Nature; you will do good for all men; you will be great; you will free men from some sicknesses and cure them of others". And out of the buried corpse of the boy arose the first Sateré-Maué.

The meaning of this myth recently became remarkably clearer. The *sorbilis* variety of guaraná grown by the Sateré-Maué is a high level polyploid, with 210 chromosomes rather than the standard 24 for the genus; the numbers and morphology of the chromosomes suggest the combination of a tetraploid and an hexaploid [118], that may be from different genera [114]. In essence, this myth captures the guaraná domestication event, which occurred when the mythological woman recognized that a special type of guaraná had become available to her, as distinct from the more common and less useful false guaraná, and that it should be planted for the benefit of future generations. True guaraná is remarkably different from the false guaranás (other *Paullinia* spp) that grow wild in the Sateré-Maué territory, so much so that any observer can readily distinguish the two morphologically by the larger fruit and seeds, and the brightly colored fruit case of true guaraná. Sexually reproducing polyploids commonly show remarkable morphological variability [3,119], which has been observed in guaraná [114,120], and may have different ecological adaptations [119], which have also been observed in guaraná, since it is well adapted to indigenous agroecosystems and does not survive long in second growth forests.

When might the domestication event have occurred? Food production systems became more important than foraging after about 4,000 years ago [121]. This time frame corresponds to the expansion of the Tupi language trunk [122], which started from what is now Rondônia in southwestern Amazonia. The Sateré-Maué may have arrived in their current location about 2,000 years ago, which provides a reasonable maximum age for the domestication event mentioned in the myth, although a Sateré-Maué elder thinks that it may have been only 600 years ago [123]. Considering that other Tupi groups in the vicinity do not consider guaraná to be as important as it is to the Sateré-Maué, it seems probable that the domestication event occurred after the arrival of the Sateré-Maué in the present location. Supporting evidence for a possibly later domestication is the lack of molecular genetic variability observed in the *sorbilis* variety among samples collected in three areas of Central Amazonia, including Maués [120], the municipality in which the Sataré-Maué live. In this study, Sousa used 16 RAPD primers to generate 150 markers (mean 9.4 markers per primer; minimum five;

maximum 13), which is reasonable for a diploid (for example, Rodrigues *et al*. [59] generated 14.1 markers per primer in peach palm). For a high level polyploid to exhibit a diploid range of bands, there must not have been mutation in the primer sequences since the polyploid event, again suggesting that it is recent. The study examined 75 clones obtained from Maués (47), Iranduba (6) and Manaus (22), and used the Dice similarity coefficient to examine the genetic relationships among these clones. The Dice similarity dendrogram showed most clones to be closely related (90% of the possible combinations had similarities greater than 0.6) and there was no geographic structuring. The lack of geographic structure suggests a recent dispersal from Maués, which is in agreement with colonial period reports that initially only the Sateré-Maué cultivated guaraná [116] and again suggests a very recent origin.

2.8. Brazil Nut

The Brazil nut (*Bertholletia excelsa* Bonpl., Lecythidaceae) is Amazonia's most important extractive product, contributing to the livelihood and food security of thousands of families in the interior of the region [124]. Brazil nut occurs as both scattered trees in upland forests and as anthropogenic stands, called *castanhais* [8,125]. Müller *et al*. [126] hypothesized that Brazil nut's current distribution is largely due to human dispersal, which is strongly supported by the distribution of *castanhais* and the lack of old growth Brazil nut in some areas, such as part of the municipality of Manaus [127] and much of the Juruá River basin [128]. Along the Purus River, in southern Amazonia, several populations have quite large seeds, suggesting incipient domestication [1].

Brazil nut's most important modern non-human seed dispersal agents are thought to be agoutis [125], small forest rodents, which are the only animals known to open the Brazil nut fruit. The choice of dispersal agents allows the elaboration of two hypotheses about Brazil nut's population structure in Amazonia, as each agent has clearly different dispersal abilities. (1) If agoutis were and are the most important dispersal agents, Brazil nut should show a fine-grained population structure, with numerous sub-populations along the interfluvials as well as through the headwaters. (2) If humans were (and are) the primary dispersal agents, Brazil nut should show a relative lack of population structure, because humans have only acted within the last 10,000 years or so, which is recent in terms of Brazil nut generations.

Ongoing work by the group led by Maristerra Lemes and Rogério Gribel, at the Instituto Nacional de Pesquisas da Amazônia, has found compelling molecular genetic evidence in support of humans as the primary dispersal agents of Brazil nut in Amazonia [129,130]. Preliminary analysis of eight widely separated populations (maximum separation 2800 km) with various chloroplast markers showed a startling lack of genetic structure. Based on chloroplast SSRs, 94% of genetic variation was found within populations, while only 6% was found among populations, which contrasts with among population variation of 10–15% in tropical tree species not propagated by humans and examined at similarly large scales (references in [131]). Several chloroplast sequences were invariable across the entire data set.

Two previous studies provide somewhat similar evidence. Buckley *et al*. [132] used several isoenzymes to examine genetic variation within and between two populations. They found only 3.75% of the genetic variation between the populations, which were less widely dispersed than the populations used by Lemes and Gribel's group. Kanashiro *et al*. [133] used 47 RAPD markers to

assess variation in five widely distributed populations, and used Shannon's H diversity index to estimate RAPD phenotypic diversity and to partition this within and among the populations. They found 31.3% of the variation among populations, considerably higher than the other studies. It is not clear why this among population measure is so different, but it may be due to the RAPD markers (which are less informative) and the Shannon index.

The sum of these studies suggests that humans distributed Brazil nut widely during the Holocene, strongly supporting Müller *et al.*'s [126] hypothesis. The anomalies in Brazil nut's modern distribution also support this hypothesis, since only human preferences can explain the absence of the species in some areas. None of these studies, however, provide any information on Brazil nut's origin. Scott Mori [134] hypothesized that Brazil nut may have originated in southeastern Amazonia. Only much more intensive population sampling and genetic analysis will permit the confirmation of this hypothesis or the elaboration of a new one.

2.9. Cupuassu

The cupuassu [*Theobroma grandiflorum* (Willd. ex. Spreng.) Schum., Malvaceae] is currently one of the most important native fruits in Amazonia, with about 35,000 ha of orchards planted over the last three decades [135]. Fruits in homegardens and orchards tend to be much larger than those collected from the forest in its reputed center of origin in southern and southeastern Pará [136], which led Clement [1] to suggest that numerous populations were incipiently domesticated before European conquest. A recent molecular genetic analysis [137] suggests that this may not be the case.

In the mid-1700s, Padre João Daniel [138] affirmed that cupuassu was not cultivated by native peoples or colonists, and suggested that its cultivation would be worthwhile. In the pre-Amazonian part of Maranhão, however, Balée [139] observed cultivation of cupuassu in Ka'apor homegardens, within the reputed center of origin of the species, although it is not known if cupuassu is a traditional crop among the Ka'apor. In the mid-1900s, Adolfo Ducke [140] (1946) commented that cupuassu was rare in western Amazonia, although it was then being dispersed along the main rivers. In fact, most cupuassu in the markets of Pará was derived from extractivism until the 1970s [135]. These somewhat conflicting observations suggest the need to reevaluate cupuassu's incipient domestication. Molecular evidence will help with this task, although only one study has been conducted to date [137].

Alves *et al.* [137] used 21 SSR loci to examine three natural populations from cupuassu's reputed center of origin in Pará (Novo Ipixuna, Tucuruí both Pará, and pre-Amazonian Maranhão), as well as three germplasm collections created separately over the last 30 years and maintained at different Embrapa stations (Amapá, Pará, Amazonas), and one extensive sample from farmers' orchards within the center of origin (Tomé-Açu, Pará). The genetic parameters estimated for these materials contained surprising patterns, with considerably less within-population diversity (70%) than expected (80–90% is common in tropical trees [131]) and considerably more among-population diversity (30%), and high levels of inbreeding ($f = 0.192$) within the three natural populations. Genetic distances among the natural populations and the farmers' orchards in the center of origin were considerable (Nei's [66] unbiased genetic distances varied from 0.198 to 0.234). This high among-population divergence may be partially due to cupuassu's pollinators (small bees and flies) and modern seed dispersal agents (small rodents), which minimize gene flow among populations, allowing genetic drift to enhance

divergence among inbred populations. The magnitudes of these genetic parameters may be a recent phenomenon, however, as cupuassu may have been dispersed by now-extinct Pleistocene megafauna [141], whose larger size may have permitted greater dispersal distances.

In contrast to these natural populations, the three germplasm collections were significantly more homogeneous (Nei's [66] distances of 0.012 to 0.033 among them), suggesting little genetic divergence over enormous distances (Amapá to western Amazonas along the Amazon and Solimões Rivers). The three collections are based upon different collection expeditions, with the Amapá and Amazonas collections containing principally state-sourced germplasm, while the Pará collection contains both state-sourced germplasm and samples from the Solimões River; there is little replication among the collections. The germplasm collections also had more alleles per population, fewer private alleles, and similar observed heterozygosities. This set of information suggests considerable gene flow over large distances, now mediated by human dispersal. Curiously, neither the Pará nor the Amapá germplasm collections had close genetic relationships with the natural populations (Nei's [66] distances of 0.350 to 0.376), suggesting that a different set of natural populations were the source of the cupuassu distributed along the main rivers during the colonial and modern periods.

This molecular analysis and the conflicting information about cupuassu's history call into question cupuassu's classification as a species with incipiently domesticated populations [1], but are not sufficient to reclassify it as wild. As cupuassu's importance increases in modern Brazilian Amazonia, new germplasm collections are planned that will hopefully permit future analyses to determine cupuassu's status as a native domesticate.

3. Patterns of Diversity

Although the number of species with molecular genetic analyses is still small, some patterns are congruent with previous thinking about the origin, domestication and dispersal of native Amazonian crops. The first important pattern is the antiquity of several important Amazonian domesticates, such as manioc (more than 8,000 BP), *Capsicum* (more than 6,000 BP), pineapple (possibly more than 6,000 BP) and, perhaps, peach palm (possibly as early as 10,000 BP). The first two have archaeological support from coastal Peru, while the latter two are projections based on morphological differences among wild and fully domesticated populations. No estimates of the dates of the primary domestication event with genetic coalescence analysis have been presented to date, but this type of analysis will certainly be attempted within the next decade.

Although these dates are quite old, they are more recent than the initial peopling of Amazonia, which occurred before 11,200 BP when the Pedra Pintada site was occupied in Central Amazonia, in what is now Monte Alegre, Pará[142]. These early occupants were broad-spectrum foragers, who may have begun domestication of the landscape near the site [143], but who did not possess any plant populations with signs of domestication. Somewhat later (7,100 BP) and on the other side of the Amazon River at Taperinha, near Santarém, Pará, settled villages appeared, based on exploitation of fluvial resources and forest foraging, as well as the first pottery in the Americas [144]. Some of the pottery suggests the presence of food production, but no evidence of domesticated plants exists [143]. Again, we can assume that landscape domestication was certainly underway. The lack of domesticated

crops in settings where dump heaps were certainly becoming home gardens [145] is curious, as at least manioc was already being dispersed from its origin in southwestern Amazonia.

This leads to a second important pattern: the relation between antiquity and origin. All but one of the species examined originated in the periphery of Amazonia (Figure 3), rather than along the major white water rivers where pre-conquest population densities were greatest. The exception is guaraná, a very recently domesticated crop, although cupuassu may be a similar case. The most important crops with domesticated populations are also the oldest, and all come from the periphery: manioc, pineapple, *Capsicum*, peach palm, tobacco, perhaps sweet potato. The importance of the periphery has been highlighted previously [121], with emphasis on extreme northwestern Amazonia and the adjacent Llanos of the Orinoco River basin, the Guiana shield and southwestern Amazonia, especially the Llanos de Mojos, in Bolivia. Work on Amazonian fruits permits the addition of numerous species with domesticated populations to the list, as well as several semi- and incipiently domesticated populations [1,146], without changing the emphasis on the periphery, although this region has now been expanded to include the Andean foothills and immediately adjacent lowlands in western Amazonia and some of southeastern Amazonia (Figure 3).

Figure 3. Confirmed and hypothetical origins of some native Amazonian crops. The confirmed origins are (from north to south): pineapple, cubiu (*Solanum sessiliflorum*), cacao, assai (*Euterpe oleracea*), guaraná, manioc, coca (*Erythroxylum coca*), tobacco (*Nicotiana tabacum*), peanut (*Arachis hypogaea*). The hypothetical origins are: genipap (*Genipa americana*), leren (*Calathea allouia*), sweet potato (*Ipomoea batatas*), cocoyam (*Xanthosoma sagittifolium*), yam (*Dioscorea trifida*), murupi pepper (*Capsicum chinense*), mapati (*Pourouma cecropiifolia*), abiu (*Pouteria caimito*), bacuri (*Platonia insignis*), inga (*Inga edulis*), cashew (*Anacardium occidentale*), sapota (*Quararibea cordata*), cupuassu, biriba (*Rollinia mucosa*), guava (*Psidium guajava*), Brazil nut, peach palm, cocoyam, annato (*Bixa orellana*), malagueta pepper (*Capsicum frutescens*). Note that there is continued uncertainty about Mesoamerican origins for guava and malagueta pepper.

Whether the peripheral origin of the earliest domesticated populations is due to the plants themselves or to human activity is an interesting question. During the terminal Pleistocene, when humans were already in Amazonia, much of western Amazonia is thought to have been forested, while

large parts of central and eastern Amazonia were open forest that was quite different from current open forests [147-149]. The drier areas along the northern and southern peripheries probably expanded further into the basin than they do currently. The crops that were domesticated early, e.g., manioc, peach palm, pineapple, probably *Capsicum*, originated in these open ecosystems, some of which remain in place, others of which have been transformed into more humid forest as this expanded during the Holocene. Some of the difficulties in identifying origins may be due to forest expansion during the Holocene, although better geographic sampling may resolve many of these difficulties.

Root and tuber crops generally originated in seasonally dry open ecosystems, where they fill their starchy storage organs before the dry season, making them attractive to hunter-gatherers during the dry season [121]. This also makes them well adapted to human modified niches in the landscape, such as dump heaps that later became home gardens [145] and incipient horticultural systems. Manioc was also selected for growth in anthropogenic soils (terra preta de índio), some of which also originated as dump heaps [150], and floodplain soils [33], although most landraces are well adapted to nutrient poor upland soils. It is probable that the other root and tuber crops also had some varieties adapted to floodplain soils, but they may have been lost in the post-conquest wave of genetic erosion that accompanied population decline [1].

The humid periphery in western Amazonia appears to be home to numerous fruit crops and different adaptations might be expected. Some, like cacao, survive well in humid forest under-stories, whereas others, like inga, have adapted well to open horticultural systems. Many of those that have not yet been subjects of genetic analysis appear to have originally adapted to successional ecotones, as they do not survive long when the second growth forest grows enough to shade them out. The exception is sapota, which is a canopy emergent when mature.

As highlighted above, however, early occupation of central Amazonia did not include domesticates, even though the ecosystems around Pedra Pintada and Taperinha were probably relatively more open at the time than currently, and landscapes within them were probably being domesticated. It is possible that sufficient natural resources were available so that the home gardens were such a small fraction of subsistence that they are difficult to find in the archaeological record. In contrast, in the headwaters of the same rivers in the periphery, less abundant aquatic resources may have increased the importance of home gardens. In fact, the earliest terra preta de índio is also in the periphery, along the Jamarí River, in the upper Madeira River basin [151]. Rindos [51] and Tudge [152] hypothesize that foragers who also practiced plant domestication would be more successful than those who did not, and it was from the southwestern periphery that two language diasporas occurred: Tupi-Guaraní and Arawak-Maipuran [122]. The southern and southwestern periphery eventually was the stage for the development of complex societies as well [153], but a detailed search is still required for signs of *in situ* crop domestication, with *Caryocar brasiliense* mentioned as a possible candidate.

A pattern whose explanation is less clear is why certain crops were widely dispersed and others not. Crops with good adaptation to environmental variation, e.g., manioc, were widely dispersed quite rapidly, appearing in the archaeological record of the Pacific coast of Peru by 8,000 BP or earlier [6] and southern Mesoamerica by 5,600 BP at the latest [154]. Those with early adaptation to human disturbance, e.g., *Capsicum*, were certainly excellent camp followers, although it is difficult to determine which peppers appear first on the coast of Peru, since only the genus is mentioned for the earliest records [6].

It is probable that ethnic preferences determined dispersal patterns. For example, peach palm's double dispersal of smaller oilier fruits down the Madeira River and along the Amazon River, and larger starchier fruits down the Ucayali River, throughout western Amazonia, along the Pacific coast of Ecuador and Colombia, and into Central America, but not the Caribbean islands, may be related to the Tupi and Arawak dispersals, respectively [53], even though these dispersals are much later than the initial domestication events. The absence of Brazil nut in the Juruá River basin is another example.

Genetic evidence also sheds light on dispersal patterns. When a domesticate was important and taken into cultivation early, generally clear genetic structuring occurs among populations, such as the landraces of peach palm. When the crop was important, early and also annual, numerous varieties were developed and spread locally, but less regional structuring is evident, as seen in manioc, although superimposed on the bitter-sweet distinction, and in *Capsicum* and pineapple. When the crop is an incipient domesticate or became important only recently, no clear genetic structuring occurs, as in Brazil nut, cupuassu and guaraná

What is quite clear, however, is that the major pre-conquest population centers concentrated crop genetic resources to guarantee their subsistence and trade (Figure 4). The major centers and regions of diversity are along the major white water rivers and in northwestern Amazonia, where ethnic diversity is extremely high [7]. The minor centers are all related to areas where pre-conquest populations transformed the landscape with earthworks of various types [7]. It may also be appropriate to consider the upper Xingu River a minor center, given the intensity of landscape domestication, complex social structure, and possible incipient domestication of local fruit trees, such as *Caryocar brasiliense* [155]. The fact that the majority of Amazonia is not included in these concentrations does not imply that crop genetic resources were absent, but that they had not been concentrated to the same degree, principally because human population densities were lower.

Figure 4. Centers, regions and minor centers of crop genetic resources diversity at the time of European conquest (modified from [7]). Centers of diversity: 1—western Amazonia; 2—central Amazonia. Minor centers: 3—Marajo Island; 4—Llanos de Mojos; 5—middle Orinoco River. Regions of diversity: 6—Solimões River; 7—upper Negro River; 8—Madeira River.
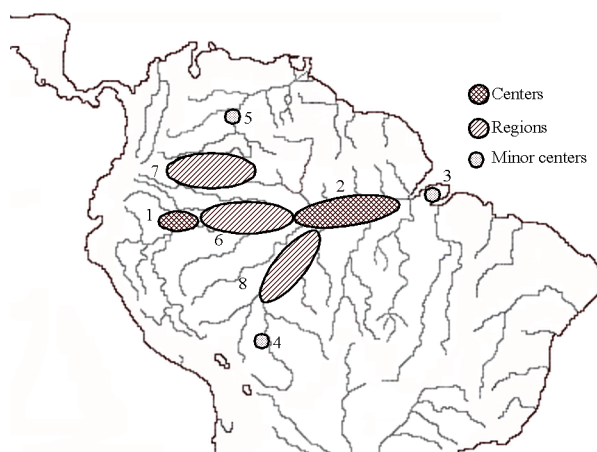
The contrast between the presumed origins of native Amazonian crops in the periphery (Figure 3) and their concentration in the centers of pre-conquest population density (Figure 4) is dramatic.

Clearly, centers of origin and centers of diversity are not equivalent concepts, as Nikolai I. Vavilov [156] understood, although many students of crop genetic resources throughout the 20th century claimed otherwise. Because crop domestication began thousands of years before food production systems became important [51,121], it is not at all surprising to see a dramatic contrast such as that in Amazonia. As the archaeology of Amazonia becomes better understood [153] and as the number of species studied with genetic and phylogeographic methods expands, we will certainly be able to clarify the patterns mentioned here and perhaps identify others.

4. Conclusions

The available information concerning the origin and domestication of manioc (*Manihot esculenta*), pineapple (*Ananas comosus*), peach palm (*Bactris gasipaes*) and guaraná (*Paullinia cupana*) is reasonably solid, while that of cacao (*Theobroma cacao*) requires rethinking presuppositions about what domestication means in that crop. The information available for hot peppers (*Capsicum* spp.), inga (*Inga edulis*), Brazil nut (*Bertholletia excelsa*) and cupuassu (*Theobroma grandiflorum*) is growing and provides substantial clues as to their origins and domestication. Emergent patterns include the relationship among domestication, antiquity, origin in the periphery, ample pre-Columbian dispersal and clear phylogeographic population structure, which often corresponds to phenotypic entities recognized by cultivators, *i.e.*, landraces (or groups of landraces), e.g., manioc, pineapple, peach palm and, perhaps, *Capsicum* peppers. Another pattern is the relationship among crops with incipiently domesticated populations, or very recently domesticated populations, rapid pre- or post-Columbian dispersal and lack of phylogeographic population structure, e.g., Brazil nut, cupuassu and guaraná Cacao represents the special case of an Amazonian species possibly brought into domestication in Mesoamerica, but close scrutiny of molecular data suggests that there may also be incipiently domesticated populations in Amazonia. Additional molecular genetic analyses on these and other species will allow better examination of these processes and will enable us to relate them to other historical ecological patterns in Amazonia.

Acknowledgements

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