Geological and Early Human Influences on Cacao Flavor

Richard Tango-Lowy and Donna McLintock

Dancing Lion Chocolate Email: richtl@dancinglion.us

ABSTRACT

While our understanding of cacao evolution and genetics has evolved dramatically over the past few decades, much of the chocolate industry, including the fine chocolate industry, still relies on obsolete and inaccurate models of cacao origin and what they imply about flavor. This paper aims to clarify how and why cacao evolved as it did, the impacts of geological and human effects on species variation, and how these have altered the flavor characteristics of some varietals more than others. Along the way, we'll address the meaning of white seed cacao: what it is, and what it isn't.

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Introduction

> *"The nomenclature of the cultivated cacaos is far from satisfactory, because many of the terms in common use (such as "Forastero", "Amelonado" and so on) do not identify unequivocally the cacaos to which they are meant to refer. ... So long as fundamental knowledge of cacao genetics is lacking, there can be neither a perfect natural classification nor an entirely satisfactory nomenclature." (Cheesman 1944)* [1] [2]

Chocolate made from different cacao varietals tastes different. It's long been known that chocolate produced from early Central American strains tends toward the fruity and nutty flavors, while that produced from western Andean strains has spicier floral notes, and eastern Amazon cacaos give chocolate a deep fudgy body. But why does cacao from specific regions often result in chocolate with identifiable flavor profiles? How did these regional flavor profiles originate?

> *"a classification of cacao based on two main populations (Criollo and Forastero) has no genetic base. Indeed, the classification based on Criollo and Forastero mentioned by Cheesman (1944) and first proposed by Morris (1882) was simply based on the terms used by the Venezuelan cacao producers of the central coastal zone." (Motomayor 2002)* [3]

Historically, cacao has been divided into three groups: *Criollo*, fine flavor cacao grown in Venezuela north to Central America and Mexico; *Forastero*, harsh or bitter cacao originating in South America; and *Trinitario*, [4] any hybrid of the former and the latter, some being of good flavor and some being less so. Recent DNA analysis, however, shows cacao is extremely rare, and nearly all trees are actually some form of *Trinitario*.

Nonetheless, the *Criollo/Trinitario/Forastero* model remains widely held within the chocolate industry.

We often encounter claims by cacao farmers, distributors, chocolate makers, and manufacturers that a particular cacao is *Criollo* or other desirable varietal. While these statements may be useful for branding and marketing purposes, without genetic validation there's no way to know that a cacao is as claimed. For instance, it is generally assumed that cacao with white seeds is pure *Criollo* and is of inherently high quality, though this is not an accurate assessment.

In 2008, a team led by Juan Motomayor applied Bayesian statistical techniques to demonstrate that cacao could be divided into 10 differentiable "clusters" of varietals, each with similar genetic characteristics.[6] While his source data contains some inherent limitations[7], this model allows cacao to be easily and accurately categorized, and provides more useful information than the ambiguous *Criollo/Trinitario/Forastero* terminology. Motomayor's team defined the unique clusters as *Amelonado*, *Contamana*, *Criollo*, *Curaray*, *Guiana*, *Iquitos*, *Maranon*, *Nacional*, *Nanay*, and *Purus*, many named for the river basins along which they most likely spread. The same data pinpoints the Upper Amazon of South America as the origin of the *Theobroma* species (Figure 2).[8]

The purpose of this paper is to trace the evolution of *Theobroma cacao* from its earliest form, *Malvacae*, and attempt to identify the most likely causes of the genetic divergences that resulted in the clusters and flavor profiles that we understand today. We will accomplish this by correlating geological and human influences with *T. cacao*'s genetic diversification. Where possible, we will connect these evolutionary divergences with chocolate flavor.

Method

To better understand cacao origin and flavor diversification, we link botanical and genetic characteristics with the most likely geographical, geological, archaeological, and anthropological influences on cacao development. We begin by creating a timeline of cacao's genetic evolution. We then overlay relevant geographical and geological events with their potential impacts on diversification, followed by archaeological and anthropological events. Finally, we correlate this data with the current understanding of genetic diversification and its impacts on chocolate flavor.

Discussion

The Evolution of Theobroma Cacao: 13 Million Years Ago to Now

12.7 million years BP (Before Present. i.e., before today), *Theobroma* and its sister *Herrania* evolved as unique members of the *Malvacaes*, the branch of the hibiscus, or mallow family that also includes cotton, linden, durian, and okra. Over the next two million years, the *Theobroma* branch split into sub-branches, including *Theobroma cacao* (**9.9 million years BP**) from which we now make chocolate (Table 1).[9] By **100,000 years BP**, *T. cacao* had diversified into at least four differentiable genetic varietals.[10] Over the past 10,000 years, *T. cacao* has undergone several further diversification events, resulting in Motomayor's ten genetic clusters. We've separated these diversification events into four distinct development phases (Figure 1):

- **Phase I:** Geographical and Geological Impacts on Cacao Diversification
- **Phase II:** Impacts of Glaciation on Cacao Diversification
- **Phase III:** Human Impacts on Cacao Diversification in the Andes and Amazon
- **Phase IV:** Human Impacts on Cacao Diversification in Central America

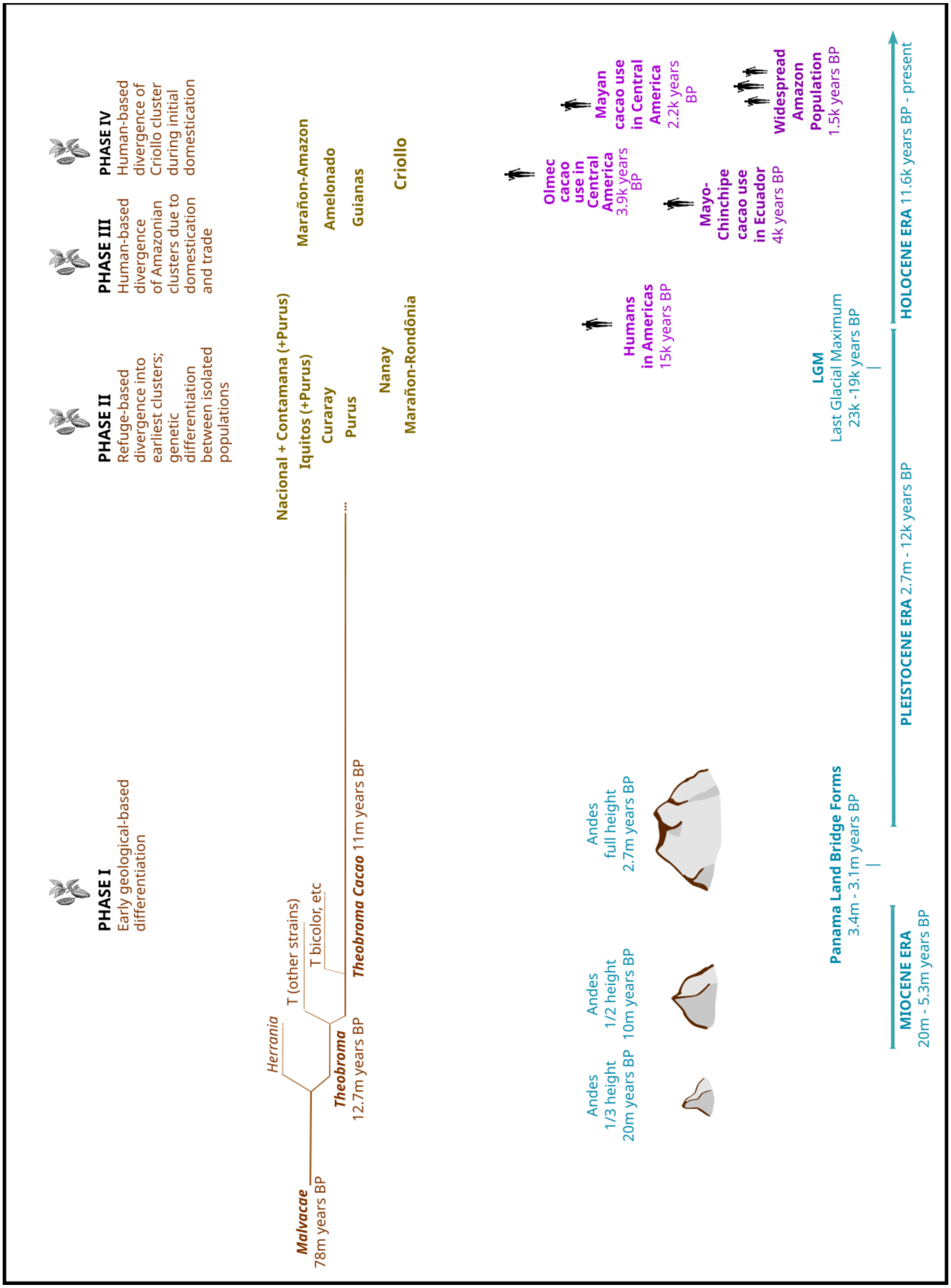

Figure 1. Theobroma Cacao Evolution Timeline from 100 million years ago to 1,000 years ago layering development phases, speciation, relevant geological events, and relevant anthropological events. Key geological events include the growth of the Andes mountain range, the Pleistocene Era and the Last Glacial Maximum (LGM); the point at which the ice age began to recede. Key anthropological events include human migration to the Americas,

Table 1. Theobroma Sub-Branches

Theobroma Sub-Branches (9.9 million years BP)	Origin in Andes
T. microcarpum, T. speciosum, T. velutinum, T. nycterodendron, T. umbraticola	East
*T. gileri, T. bicolor, **T. cacao**, T. nitida, T. cuatrecasana, T. kanukuensis, T. purpurea, T. albiflora*	**West & East**
T. mammosum, T. angustifolium, T. chocoense, T. similarum, T. grandiflorum	West

Phase I: Geographical and Geological Impacts on Cacao Diversification

Herrania and *Theobroma* developed in the upper Amazon River basin on what is now the border between Peru, Brazil, and Colombia, [11] and spread through the region along existing waterways. Prior to the growth of the Andes Mountains **20 million years BP**, the Amazon River flowed inland, creating a wetland hospitable to early tropical plant life. [12] As the Andes Mountain chain grew, **20 million to 2.7 million years BP**, groups of *Theobroma* trees became separated by rising mountainous ridges. Over the next ten million years, during the Miocene and the first half of the Pleistocene periods, microclimate differences in these regions caused *Theobroma* to speciate, or begin developing into unique genetic varietals.

Figure 2. Center of Origin. Over the years, several theories have placed the origin of *T. Cacao* in Mexico, Central America, and South America. Modern research places the origin fairly conclusively at the point of greatest genetic diversity: the upper Amazon basin on the borders of what are now Colombia, Peru, and Brazil. Diagram courtesy of *Dancing Lion Chocolate*.

Phase II: Impacts of Glaciation on Cacao Diversification

From the Last Glacial Maximum (LGM), **23,000 to 19,000 years BP**, until the end of the ice age, *T. cacao* survived in isolated warm pockets, or "refuges" in the western Amazon. Local adaptations over many generations caused these individual populations to speciate yet more quickly, resulting in dramatic genetic diversity. [13] By the end of this period, *T. cacao* had evolved into four differentiable genetic groups, *Nacional + Contamana + Purus*, *Iquitos + Purus*, *Curaray*, and *Purus* [14], and was beginning to resemble the varietals we see today. (Table 2, Figure 3)

Table 2. Genetic Clusters and Origins

Phase	Clusters Defined by Thomas	Clusters Defined by Motomayor	Probable Origin	Cluster Number
I,II	Nacional + Contamana (+Purus)	Contamana	Ucayali River, Central Peru	6
I,II	Iquitos (+Purus)	Iquitos	Upper Amazon Basin, Northwestern Brazil	8
I,II	Curaray	Curaray	Western Amazon Basin, Ecuador	10
I,II	Purus	Purus	Purus River, Western Brazil near Peru	1
III	Marañón-Amazon	Maranon	Marañón River, Peru	4
III	Amelonado	Amelonado	Bahia, Brazil from southeast of Guiana	5
III	Nanay	Nanay	Northern Amazon Basin, Peru	9
III	Guianas	Guianas	Southeast of Guiana	3
III	Marañón-Rondônia			7
IV	Criollo	Criollo	Central America via northwest South America	2

Phase III: Human Impacts on Cacao Diversification in the Andes and Amazon

It is currently accepted that the first humans in the Americas arrived by boat from Beringia, on the Bering Strait, and migrated south along the coast to North America, Central America, and finally South America.[15][16] Excavations indicate that humans had settled in multiple locations in the Americas by **15,000 years BP** at the latest, but probably at least 5,000 years prior.[17][18][19]

> *"evidence [of cacao trade] appears from the headwaters of the Chinchipe River, near the town of Valladolid; around the town of Amaluza in Loja province; and near the border in Zumba (Ecuador). On the other side of the Peru-Ecuador border, these remains have been found in San Ignacio and Jaén all the way to where this river meets the Marañón, near Bagua..." (Unesco 2016)*[20]

Evidence of the earliest documented cacao consumption by humans was found in DNA samples in pottery dating back 4,000 years, found at the Santa Ana-La Florida (SALF) site in Ecuador. The pots and vessels were created by the Mayo-Chinchipe-Marañón people (**7,500 to 3,750 years BP**), who likely used cacao as a source for nutritional fat and as a fermented beverage. The Mayo-Chinchipe-Marañón traded goods extensively through the region: some vessels contain images of bivalves that exist only between Baja and the north coast of Peru, indicating trade along the coast,[21] and fragments of their pottery have been found from the Pacific Coast to the Andean Highlands to the Amazon Lowlands. Evidence of trading as far as the Marañón River headwaters indicates that they were likely involved in the domestication of multiple cacao varietals, from *Nacional* to *Marañón*, and they might well have been responsible for bringing *Nacional* cacao to the Ecuador coast.

Amelonado and *Guianas* have significant genetic overlap and it's likely that human intervention brought *Amelonado* from southeast of Guiana to the Bahia area in eastern Brazil. USDA research leader Lyndel Meinhardt writes "We have found wild *Amelonado* just Southeast of Guiana in Brazil and data suggest the original source of *Amelonado* to Bahia came from this region." He goes on to specify that both of these clusters are genetically separate from Upper Amazon cacao.[22]

Phase IV: Human Impacts on Cacao Diversification in Central America

As people settled inland, they brought and traded the early *Criollo* cacao they encountered on the northern west Andean coast up along the Panama isthmus into Central America,[23] where it began to develop independently from other varietals.[24] (Figure 3)

By **4,500 years BP** the Olmec people of Central America had domesticated some of this *Criollo* cacao (Table 3, Figure 4), and by **3,900 years BP** there's evidence of the use of cacao beverages, though current techniques make it impossible to determine if these were made from fermented cacao pulp or what we now know as "chocolate."[25] Separation of seeds from pulp, along with changes to vessel shapes, appears to indicate the shift from the former to the latter at least **3,000 years BP**, possibly earlier[26]. The Olmecs, followed by the Mayans and then the Aztecs, continued to actively hybridize and develop cacao to improve the flavor of their chocolate beverage, which the Mayans called *chikolatl*,[27] The intensive domestication resulted in *Criollo* cacao being highly differentiated from the other clusters. One result of this intensive inbreeding was the frequent occurrence of the white seed, or anthocyanin mutation, which yields less bitterness, though also less vigorous trees.[28]

Table 3. Early Cacao Use in the Americas

Chocolate Use in the Americas	Site	Date Range
Assorted vessels	Santa Ana - La Florida SALF, Ecuador (Mayo-Chinchipe-Marañón)	7,500BP - 3,700BP
Tecomate (neckless jar)	Paso de la Amada (Mokaya)[29]	3,900BP - 3,500BP
27 vessels	San Lorenzo, Mexico (Olmec)[30]	3,800BP - 3,000BP
	El Manatí, Mexico (Olmec)	3,650BP
Jars, bottles, spouted vessels	Puerto Escondido, Honduras[31]	3,400BP - 2,200BP

Figure 3. Cluster Origins and Migration Paths. Clusters of genetically similar varietals are generally associated with their nearest river drainage basins, as that's how they tended to propagate. *Nacional*, *Marañón*, *Criollo*, and *Amelonado* were most likely spread by human domestication and trading, where they formed evolutionary bottlenecks in isolation from other varietals. Map copyright *d-maps* (https://d-maps.com/pays.php?num_pay=120), overlay by *Dancing Lion Chocolate*.

Figure 4. Theobromine-containing vessels from Paso de la Amada, a Mokaya site dated to at least 3,500 years BP. Image courtesy of Alejandro Linares Garcia - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=15208854

Connecting Cacao with Flavor

How Genetics Affects Flavor

> *MYTH: Criollo cacao makes the best chocolate, and other varietals are not as complex or nuanced.*

Although geology and geography drove the initial genetic diversification in cacao, the most significant impacts on cacao flavor were caused by humans. Through trading and domestication, early South and Central American peoples selected and relocated preferred varietals, resulting in low genetic diversity. *Criollo* cacao, for example, evolved almost entirely through human intervention in Central America, where it was likely the dominant or even only varietal present for several thousand years. *Amelonado* cacao was spread from the Pará River of Brazil southward along the east coast, also in isolation. As we've seen, the Mayo-Chinchipe-Marañón people traded *Nacional* and *Marañón* cacao between the western Andes mountains and Marañón river headwaters and into the Marañón Cañon, again creating isolated populations. Each of these domesticated strains contains the potential for chocolate with specific flavor characteristics.

The **Heirloom Cacao Preservation Fund** (HCP) provides data that enables us to loosely correlate genetics with standardized tasting notes for chocolate made using a consistent production process. [32] There are 16 Heirloom designees at the time of this article, each recognized for supplying cacao "endowed with a combination of historic, cultural, botanical, geographical and flavor value that is the foundation of the best tasting chocolate." Although the sample size (n=16) is small, it is possible to make some coarse generalizations. We've added our own observations in italics, based on our experience as an artisan chocolatier and chocolate maker.

- Cacao high in **Criollo** content (Table 4a) tends toward mild chocolate flavor with strong panela and caramel sweetness and minimal bitterness. *Typically moderate-to-full body with low acidity and astringency.*
- Cacao high in **Amelonado** content (Table 4b) tends toward pronounced fruit notes and fruit acidity, with mild nut-skin astringency. *Typically full-body with honey sweetness.*
- Cacao high in **Nacional** content (Table 4c) tends toward nutty caramel notes, low bitterness, and velvety astringency.
- Cacao high in **Forastero** [33] content (Table 4d) tends toward moderate chocolate flavor with mild fruit acidity and balanced bitterness and astringency. *Typically spice notes with light to medium body.*
- Cacao high in **Boliviano** [34] content (Table 4e) tends toward moderate chocolate flavor with tart fruit and floral notes and some acidity.

Table 4a. Criollo Flavor Correlation (70% or higher Criollo content)

Designee, Location	Genetic Makeup	HCP Taster Panel Highlights
11, Belize	100% Criollo	Mild chocolate. Roasted nuts. Caramel and panela. Lightly floral.
15, Madagascar	71% Criollo, 24% Amelonado	Mild chocolate. Fresh tart fruit. Caramelized sugar, panela, and toffee. Tart fruit acidity. Mild nut skin astringency.
	Characteristics	*Mild chocolate flavor, strong panela and caramel flavors, minimal bitterness*

Table 4b. Amelonado Flavor Correlation (55% or higher Amelonado content)

Designee, Location	Genetic Makeup	HCP Taster Panel Highlights
1, Bolivia	58% Amelonado, 18% Criollo, 16% Forastero	Rich and powerful, tart and browned fruits, dark cherry and currants. Mild astringency.
8, Nicaragua	70% Amelonado, 27% Criollo	Mild chocolate. Bold fresh fruit. Nut skin notes. Strong fruit acidity.
12, Nicaragua	56% Amelonado, 23% Criollo	Fresh fruits of all types. Honey and molasses. Nut skin finish. Strong fruit acidity, mild astringency.
16, Philippines	58% Amelonado, 38% Ucayali	Mild chocolate. Mildly tart berries and citrus. Sweet caramel and toffee. Balanced acidity, bitterness, and astringency.
	Characteristics	*Pronounced fruit notes and fruit acidity, mild nut-skin astringency*

Table 4c. Nacional Flavor Correlation (55% or higher Nacional content)

Designee, Location	Genetic Makeup	HCP Taster Panel Highlights
3, Ecuador	63% Nacional, 17% Amelonado, 17% Forastero	Mild chocolate, nutty, caramel. Low bitterness and astringency.
5, Ecuador	55% Nacional, 31% Amelonado	Strong chocolate, caramel and nutty. Mild acidity, velvet astringency.
9, Ecuador	72% Nacional, 17% Amelonado	Strong chocolate. Browned dates and raisins; molasses. Herbal notes. Mild bitterness, velvet astringency.
	Characteristics	*Nutty caramel notes, mild bitterness, velvety astringency*

Table 4d. Forastero Flavor Correlation (35% or higher Forastero content)

Designee, Location	Genetic Makeup	HCP Taster Panel Highlights
6, Costa Rica	38% Forastero, 32% Amelonado, 16% Criollo	Balanced chocolate. Berries, currants, and raspberries. Fresh fruit acidity. Balanced bitterness and astringency.
7, Belize	41% Amelonado, 36% Forastero	Moderate chocolate. Strong fruit and caramel notes. Mild fruit acidity, low bitterness, velvet astringency.
	Characteristics	*Moderate chocolate, mild fruit acidity, balanced bitterness and astringency.*

Table 4e. Boliviano Flavor Correlation (97% Boliviano content)

Designee, Location	Genetic Makeup	HCP Taster Panel Highlights
2, Bolivia	97% Boliviano	*Moderate chocolate, tart fruit, floral notes. Moderate acidity.*

While some or all of the remaining clusters might be associated with unique flavor characteristics, until we are able to locate and taste chocolate from pure wild strains, it is difficult or impossible to identify whether those characteristics exist or what they might be.

It's critical to note that *the genetics of a cacao varietal provide the molecular precursors that carry the potential for chocolate flavor*, but the actual flavor is influenced strongly by both terroir and the chocolate making process.

How Terroir Affects Chocolate Flavor

> *""[Terroir] represents sensory qualities of food that capture a dynamic engagement between people, place and taste." (Trubek 2008)* [35]

The unique flavor of any cacao is influenced by the soil, water, and sunlight, the yeast, air, people, and process.

Scientists debate whether mineral content and soil composition affect the flavor of growing plants. Studies of wine grapes show that soil composition doesn't actually affect taste, [36] but studies of tomatoes show that soil composition, particularly the amount of sulfur present, can dramatically improve flavor. [37] While it's likely that soil has an impact on cacao flavor, we know little about how it might produce better-tasting chocolate.

According to John Havlin, professor and extension specialist at North Carolina State University, climate and growing conditions, specifically rainfall and daily temperatures, impact flavor more strongly than does soil. [38] Cacao trees flourish in warm, gently moist conditions. Each year Dancing Lion Chocolate receives a batch of Guatemalan chocolate from chocolate maker Carlos Eichenberger, owner of *Danta Chocolate* in Guatemala City. Over the years, we've noticed that chocolate harvested after a rainy season has a stronger coffee flavor than chocolate harvested after a dry season. The effect is so pronounced, we've learned to estimate the rainfall of the season by the taste of the chocolate.

Cacao grows best in the shade, so the impacts of sunlight are less dramatic than in wine grapes. Nonetheless, University of Florida researcher Anna-Lisa Paul points out that “the balance of those wavelengths and their intensity can have a big effect on the composition of its ‘secondary compounds,’ chemicals that contribute to taste.” [39]

> *"Yeasts come in from the rainforest and the chocolate tastes one way. The next day, yeasts blow in from the ocean and the chocolate tastes another." Dr. Howard Yana-Shapiro, Chief Agricultural Officer & Mars Fellow at Mars, Inc.* [40]

But terroir is more than soil, climate, and sunlight; place is also about culture. Cacao must be fermented and dried before being processed into chocolate, and people play a part in this process. In most locations, pulpy seeds from the cacao pod are fermented in stacked wooden boxes covered with banana leaves, but there are many variations. After fermentation, the cacao must be dried. The type of wood used for the boxes, the yeasts in the air,[41] the materials used to cover the pulp, where and how the cacao is dried, and the habits and techniques of the workers all contribute to chocolate flavor. *The fermentation and drying processes influence and alter the molecular precursors within the cacao.*

Impacts of the White Seed / Anthocyanin Mutation

> *MYTH: The best-quality cacao is white-seed Criollo, and white seeds exist only in high-quality Criollo cacao.*

Most unfermented cacao seeds are deep purple-blue when cut. This coloration is due to the presence of anthocyanins, a class of polyphenols that lend the same color to currants, purple cabbage, blackberries, and wild blueberries. Anthocyanins also contribute bitterness and astringency, which is why most cacao is somewhat bitter and astringent.[42]

As mentioned above, intensive inbreeding of a cacao variant results in the increased expression of the recessive white seed trait in that variant. While white seeds are typically associated with *Criollo* cacao, this is probably because *Criollo* was highly inbred due to its isolation in Central America and early domestication by the Olmecs and Mayans. In fact, *Marañón Cañon* cacao is a white seed *Nacional* varietal, and *Brazilian Catongo* is a white seed *Amelonado*. The white seed trait in all three is most likely due to human-induced evolutionary bottlenecks in those varietals.

Because the white seed expression is caused by a lack of anthocyanins, *all* white seed cacao tends to be low in bitterness and astringency, regardless of varietal.

Discussion

Our understanding of cacao origins and evolution has changed significantly over the past several decades. New tools and research methods have given us more accurate insights into the correlation between cacao genetics, origin, and flavor. For example, techniques such as Bayesian statistical analysis make it possible to group cacao into genetically similar clusters based on commonalities in DNA. Current research by the USDA (United States Department of Agriculture) aims to further improve models by better correlating cacao samples with specific GPS locations.

Research by Motomayor, Thomas, and others has made it clear that cacao originated in the upper Amazon basin of South America, rather than in Central America or both locations as was previously hypothesized. The species spread through waterways within the pre-Andean wetlands and began to genetically diversify as the Andes Mountain range formed and then later within warm refuges during the glacial period.

Early human trading and domestication contributed to cacao flavor by creating evolutionary bottlenecks, where affected species developed in isolation from other species. This isolation caused an anthocyanin recessive trait to become prominant, resulting in cacao with white seeds and low bitterness and astringency. While white seed cacao is most common in Central American *Criollo* varieties, it has also been demonstrated in *Nacional* and *Amelonado*, and can likely exist in any cacao given enough time and sufficiently isolated domestication.

Based on our understanding of cacao evolution and genetics, it is possible to draw a loose relationship between cacao origin and chocolate flavor. There is limited data available to solidify this correlation, and the dramatic impacts of terroir on flavor make the relationship especially complex. Nonetheless, the correlation can be made, particularly in the case of varietals that have undergone evolutionary bottlenecks; specifically within the *Criollo*, *Nacional*, and significantly benefit the fine chocolate industry. The work performed by the **Heirloom Cacao Preservation Fund (HCP)** is critical in this regard.

This paper examines cacao as it developed prior to the arrival of the Spanish in the Americas. For an extensive treatise on post-Columbian cacao development, we recommend *"Review of Cacao Exploration and Germplasm Movements"* by Lambert A. Motilal, published by HCP in 2022.[43]

Appendix. Table of Heirloom Cacao Designees with Genetic Makeup and Tasting Panel Summary

Table 5. HCP Derived Data

HCP Designee and Location	Genetic Makeup	Tasting Panel Report - Dominant Notes
1 - Bolivia	58% Amelonado, 18% Criollo, 16% Forastero	Rich and powerful, tart and browned fruits, dark cherry and currants. Mild astringency.
2 - Bolivia	97% Boliviano	Moderate chocolate, tart fruit, floral notes. Acidity.
3 - Ecuador	63% Nacional, 17% Amelonado, 17% Forastero	Mild chocolate, nutty, caramel. Low bitterness and astringency.
4 - Hawaii	38% Amelonado, 33% Forastero, 20% Criollo	Moderate chocolate; raisins, plums, and figs. Some acidity.
5 - Ecuador	55% Nacional, 31% Amelonado	Strong chocolate, caramel and nutty. Mild acidity, velvet astringency.
6 - Costa Rica	38% Forastero, 32% Amelonado, 16% Criollo	Balanced chocolate. Berries, currants, and raspberries. Fresh fruit acidity. Balanced bitterness and astringency.
7 - Belize	41% Amelonado, 36% Forastero	Moderate chocolate. Strong fruit and caramel notes. Mild fruit acidity, low bitterness, velvet astringency.
8 - Nicaragua	70% Amelonado, 27% Criollo	Mild chocolate. Bold fresh fruit. Nut skin notes. Strong fruit acidity.
9 - Ecuador	72% Nacional, 17% Amelonado	Strong chocolate. Browned dates and raisings; molasses. Herbal notes. Mild bitterness, velvet astringency.
10 - Ecuador	39% Nacional, 23% Ucayali, 21% Amelonado	Moderate chocolate. Woody and resinous. Spice finish. Strong citrus acidity, mild astringency.
11 - Belize	100% Criollo	Mild chocolate. Roasted nuts. Caramel and panela. Lightly floral.
12 - Nicaragua	56% Amelonado, 23% Criollo	Fresh fruits of all types. Honey and molasses. Nut skin finish. Strong fruit acidity, mild astringency.
13 - Vietnam	47% Parinari, 29% Criollo	Strong chocolate. Browned fruit, coconut with spices. Bitter almond acidity.
14 - Tanzania	32% Amelonado, 25% IMC, 15% Criollo	Strong chocolate. Tart fresh fruits. Browned raisins and dates. Dark molasses and wood. Spice finish. Tart fruit acidity.
15 - Madagascar	71% Criollo, 24% Amelonado	Mild chocolate. Fresh tart fruit. Caramelized sugar, panela, and toffee. Tart fruit acidity. Mild nut skin astringency.
16 - Philippines	58% Amelonado, 38% Ucayali	Mild chocolate. Mildly tart berries and citrus. Sweet caramel and toffee. Balanced acidity, bitterness, and astringency.

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1. E. E. Cheesman (1944) *"Notes on the Nomenclature, Classification and Possible Relationships of Cacao Populations"*.Tropical Agriculture Vol. 21 No. 8: 144 ↩

2. Much gratitude to Mark Christian of C-Spot and Dr. Gideon Ramtahal of the Cocoa Research Center (CRC) of the West Indies for assistance in obtaining a copy of E. E. Cheesman's original 1944 paper. ↩

3. JC Motamayor, AM Risterucci, PA Lopez, CF Ortiz, A Moreno, C Lanaud (2002) *"Cacao domestication I: the origin of the cacao cultivated by the Mayas"*. eredity

5. Dapeng Zhang, Michel Boccara, Lambert Motilal, Sue Mischke, Elizabeth S. Johnson, David R. Butler, Bryan Bailey, and Lyndel Meinhardt (2008) *"Molecular characterization of an earliest cacao (Theobroma cacao L.) collection from Upper Amazon using microsatellite DNA markers"* Tree Genetics & Genomes (2009) 5: 604 ↩

6. Juan C. Motamayor, Philippe Lachenaud, Jay Wallace da Silva e Mota, Rey Loor, David N. Kuhn, J. Steven Brown, Raymond J. Schnell (2008) *"Geographic and Genetic Population Differentiation of the Amazonian Chocolate Tree (Theobroma cacao L)"* PLoS ONE 3(10) e3311: 2 ↩

7. According to Lyndel Meinhardt of the USDA, the dataset that Motomayor used for research was collected pre-GPS, so the physical location of the data points is questionable. "If you don’t know for sure where the samples came from it is hard to locate a population. Thomas used the same data to develop his manuscript, so any bad passport data is further propagated in Thomas' work." ↩

8. Motamayor, et al (2002) *"Cacao domestication I"*: 384 ↩

9. James E. Richardson, Barbara A Whitlock, Alan W. Meerow, Santiago Madrinan (2015) *"The age of chocolate: a diversification history of Theobroma and Malvacae"* Frontiers in Ecology and Evolution: 1 ↩

10. Evert Thomas, Maarten van Zonneveld, Judy Loo, Toby Hodgkin, Gea Galluzzi, Jacob van Etten (2012) *"Present Spatial Diversity Patterns of Theobroma cacao L. in the Neotropics Reflect Genetic Differentiation in Pleistocene Refugia Followed by Human-Influenced Dispersal"* PLoS ONE 7(10): 10-11 ↩

11. ibid: 10 ↩

12. Richardson, et al: 1-2 ↩

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14. Thomas, et al: 9-11 ↩

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33. From discussions with Lyndel Meinhardt: "Upper Amazon Forastero refers basically to the populations west of Iquitos. It could refer to a hybrid mix or to a single population." ↩

34. HCP designees #1 and #2 are from wild cacao harvested in Alto Beni, Bolivia, and the latter appears to be a unique genetic varietal. Lyndel writes "Alto Beni and Chuncho (Peru) are probably the same population group since both are from the Madeira River waterway that runs along the border of Rondonia before branching into Peru and Bolivia." ↩

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