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'Moving South': Late Pleistocene Plant Exploitation and the Importance of Palm in the Colombian Amazon

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Abstract: The role of plants in early human migrations across the globe has received little attention compared to big game hunting. Tropical forests in particular have been seen as a barrier for Late Pleistocene human dispersals due to perceived difficulties in obtaining sufficient subsistence resources. Archaeobotanical data from the Cerro Azul rock outcrop in the Colombian Amazon details Late Pleistocene plant exploitation providing insight into early human subsistence in the tropical forest. The dominance of palm taxa in the assemblage, dating from 12.5 ka BP, allows us to speculate on processes of ecological knowledge transfer and the identification of edible resources in a novel environment. Following the hypothesis of Martin Jones from his 2009 work, "Moving North: archaeobotanical evidence for plant diet in Middle and Upper Paleolithic Europe", we contend that the instantly recognizable and economically useful palm family (Arecaceae) provided a "gateway" to the unknown resources of the Amazon forest.

Keywords: Amazon; Late Pleistocene; archaeobotany; palm; ecological knowledge; plant exploitation; peopling South America

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1. Introduction

Early hunter-gatherer diet is a key topic for understanding human ecology and evolution, providing insight into the origins of the interactions between people and their environment and the development of foodways as part of Pleistocene global human expansion. Discussions of hominin and human colonization of different continents and environments during the Pleistocene often have a tendency to focus on the ways in which societies were able to procure animal resources. More specifically, discussions of human migration out of Africa and around the world have been linked to the development and application of more sophisticated technologies and hunting strategies, including the bow and arrow [1–3]. However, the role of plants in these early migrations of our species has received less attention, with greater focus on the later domestication of cultigens and the transition to agriculture [4–7]. Where plants have been discussed in early colonizations, the focus has typically been on the potential availability of edible resources and the limitations of the habitat, especially for tropical forests [8,9], with little discussion of the behavioral processes that enabled pioneers to successfully exploit plants when entering new environments.

In 2009, Martin Jones wrote the paper "Moving North: archaeobotanical evidence for plant diet in Middle and Upper Paleolithic Europe" [10], in which he reviewed the evidence for the role of plant foods in the northward expansion of *Homo sapiens* in Palaeolithic Europe. He argued that the plant component of diet is essential to dilute the nitrogen load from animal protein and that a crucial part of the latitudinal expansion of *Homo sapiens* was tied up with the ability to acquire sufficient plant foods in the novel environments that the first generations of humans crossed and colonized. Jones [10] discusses the development and deployment of an "ecological intelligence" in foraging decisions through transferable knowledge as new environments are encountered. The ability to rapidly identify key physical traits in newly encountered plant taxa that share similarities with known edibles potentially enabled the successful adaptation to the new environments. This forefronting of botanical knowledge and resources in Pleistocene dispersals of *Homo sapiens* has remained limited beyond this seminal work.

Discussions of the peopling of South America have tended to be dominated, as elsewhere in the Pleistocene world, by assumptions that humans preferred coastal and savanna settings [11,12]. By contrast, tropical forests, like those in the interior of South America, have been seen as barriers to early human foragers due to the difficulties in obtaining sufficient nutrition from hunting and foraging activities [8,9]. A growing body of research, however, is transforming our understanding of subsistence practices and migratory choices of pioneering settlers in the region [13–18]. Indeed, arrival in South America appears to represent a virtually unprecedented migration of modern humans across richly diverse landscapes during the late Pleistocene-early Holocene (LP-EH) transition (ca. 16–11 ky BP). Here, humans encountered a wide diversity of challenging environments including savannas, high Andean plateaus, inter-Andean valleys, and even the lowland forests of the Amazon [17,18], within a relatively small distance, offering a wealth of unknown edible plant species, and early evidence of human activity has been found across these settings [18–25]. Archaeobotanical studies are providing a far greater appreciation of plants in the diet of these early settlers in the neotropics [13–16,18,23,25] and elsewhere in South America [26,27], although processes of human decision-making and the development of adaptive strategies in plant exploitation remain understudied.

Here, we explore the evidence for plant exploitation during the southward human migration into South America, with a focus on the Serranía la Lindosa (SLL) in the Colombian Amazon. We review palaeobotanical, zooarchaeological and archaeological evidence from the recently discovered earliest human contexts in the Colombian Amazon at Cerro Azul [18], where evidence beginning ~12,600 cal BP contribute to our understanding of the initial colonists' diet and subsistence choices in the Amazon Basin. These results demonstrate the importance of palm exploitation for the early settlers, addressing core processes of human ecology and evolution in tropical forest settings and laying the foundation for later subsistence developments. We discuss the evidence for plant foraging strategies and speculate on the role of visually distinct palms in facilitating entry to the Amazon forest. The process mirrors the European palaeolithic example discussed by Jones [10], albeit in the reversed direction, as ecological knowledge transfer in subsistence decisions enabled humans to "move south" into one of the last frontiers of human tropical colonization.

Theoretical Background

The central tenet of Jones' manuscript highlights that the challenge of acquiring plant foods and the growing need for multi-stage processing for edible plant material increased with northward expansion. Jones identifies three principal obstacles with progressively northerly latitudes in Europe: (1) soft, edible, plant tissue production becomes increasingly seasonal and available for shorter times during the year, (2) total biomass productivity in the ecosystem is lower, and (3) there is an increase in defensive mechanisms of plants, including toxins, spines, and other barriers to digestion. To overcome these issues, Jones speculates that certain visually distinctive traits of plant families may have facilitated the cross-ecosystem identification of edible species in newly encountered habitats, even when the actual known species are not present. This ecological intelligence enabled the transfer of ecological knowledge and low risk experimentation between distinct ecosystems and their plant assemblages.

Two examples cited are the similarities of seed pods amongst legumes and the distinctive parallel veined leaves of monocots. The seeds of legumes have been a major food source throughout hominin evolution and taxa from the family are represented across a vast geographical and ecological range [28]. The fruiting pods of leguminous plants are visually similar amongst the wide diversity of plants in the taxonomic family and could have been an easily identifiable potential food source [10]. Likewise, the parallel veins of monocot leaves may have acted as a visual guide to plants with potential to yield edible material. Globally, monocots are an essential part of the hominin diet, and more specifically, human foodways and culture [29]. They include major grains (rice, wheat, maize, etc.), grasses (sugar cane, bamboo, etc.), palms, and many other edibles (e.g., ginger, plantain, onion, garlic, etc.). The edible portion of monocots varies between taxa, from the tips of the stem and fruits (e.g., palm) to underground tubers and rhizomes (e.g., *Dioscorea* (yams)). Despite diversity amongst taxa, the distinct leaves may act as a salient visual clue to the high dietary potential of a newly encountered species. Thus, when faced with a new landscape and unknown plants, key visual clues, such as leaf veins and seed pods, may have facilitated successful human occupation and adaptation [10].

The European Palaeolithic example discussed by Jones provides a useful simple conceptual model, although it is problematic to directly apply to Pleistocene human expansion into South America. Firstly, the initial colonization of South America occurs fully within tropical latitudes. The stark climatic and ecological changes with latitude across temperate Europe are conducive to such a broad, linear characterization, whereas the tropical latitudes encompass less variability in temperature and daylight hours. Furthermore, the Andean mountain chain adds complexity to simple latitudinal discussions of 'moving south'. As humans arrived in northwest South America they would have found significant landscape heterogeneity reflected in the topography, climate and vegetation that is more closely related to the altitudinal gradients of the montane chain, rather than latitude. Thus, perhaps the greatest challenges faced during the human expansion into northwest South America and Amazonia were: (1) the highly contrasting environments colonists immediately faced upon entering South America, and before entering the Amazon region, and (2) the instability of environments during the LP-EH transition. The core concern of Jones [10], regarding the challenge of procuring plant foods in a new environment does, however, remain, and "moving south" into the tropical forests of the region provides an ideal context to see if the same processes of ecological knowledge transfer occur in the opposite direction.

Although tropical forests have high biomass production and biodiversity, they have been argued to represent a barrier to early pre-agricultural humans (see [30,31]). It has been suggested that hunting, gathering and fishing, in the absence of independent cultivation of domesticated crops, could not provide enough resources to permanently sustain human populations [8,32]. In particular, a scarcity of fat and protein-rich fauna and carbohydrate-rich plants was postulated to prohibit successful subsistence practices based on foraging [8,9,33]. Despite high biomass, productivity and species diversity, most of the energy in a tropical forest exists in inedible woody tissue, with proportionally little energy available for human consumption. Edible fruits and nuts are often high in the canopy, out of reach of bipedal human foragers, and highly dispersed in space requiring intensive labor and time inputs [8]. Furthermore, scarcity and seasonality of wild starch foods made tropical forests food-poor ecosystems for hunter-gatherers. Ultimately, these challenges, alongside a lack of ethnographic examples of pure hunter-gatherers led to a stereotypical view that tropical forests could not support pre-agricultural communities.

While these concerns do carry weight, research has demonstrated that tropical game can be fat-rich and many plant resources are carbohydrate-rich, with archaeological examples also demonstrating that specialized tropical foraging has been successful in deep time (see [34] for discussion). Headland and Bailey [31] do point out that the lack of clear ethnographic examples of pure hunter-gatherer subsistence was compounded by the legacy of past human impacts on forest composition and resource availability [31]. Modern hunter-gatherers were thus benefiting from the impacts of plant and animal domestication and past forest management. The discovery and analysis of LP-EH contexts in tropical forest settings, prior to crop cultivation, is therefore essential to understanding human ecology and evolution. The recent analysis of LP archaeological sites in the Serranía la Lindosa in Colombia evidences a thriving culture engaged in hunting, gathering and fishing, thousands of years before crops were domesticated and agriculture adopted [18]. This context presents the opportunity to explore concepts of ecological knowledge transfer in migratory decisions to new ecosystems and how pioneering settlers overcame the challenges of food procurement in tropical forests.

2. Geographical and Archaeological Background

2.1. Geographical Setting

Climate change and its impact on different environments and landscapes played a significant role in global human dispersals during the Late Pleistocene era [35–38]. This was particularly the case for the first humans to enter South America during a period of gradual deglaciation following the Last Glacial Maximum (LGM) (23–19 ka BP) as well as the abrupt climatic episodes of the dry Heinrich Event (H1) (17–16 ka BP) and the return to glacial conditions of the Younger Dryas (YD) ~12.9–11.5 ka BP [39,40]. Compared to today's climate, the Neotropics were at least 6 °C cooler and received 30–50% less precipitation during the Late Pleistocene [6], while the global climate also meant sea-levels were over 100 m lower [41,42]. During the LP-EH transition, Andean tree lines shifted, ecotone boundaries between savanna and seasonal forests moved and lowland ecosystems underwent fluctuations in their vegetation composition [43,44]. Vegetation change, in turn, had profound implications for animal habitats, with serious consequences for the now extinct megafauna [45].

These changes on the landscape meant that a process of learning and innovation in technological practices was required by incoming humans to negotiate the range of local landscapes undergoing change. The first human arrivals to South America were geographically forced to pass through the bottleneck formed by the Isthmus of Panama and the Darien Gateway. Migrating humans would have had the opportunity to encounter any potentially unavoidable transit through humid tropical forests during their passage through Central America. This would have enabled, or necessitated, the development of ecological knowledge specific to the humid forest. Whether these Central American migrants were able to employ these specific skill sets in the Amazon, or potentially pass on knowledge through successive generations remains unknown. At present, archaeological evidence suggests the early migrants followed a Pacific coastal route through now submerged landmass [46]. A central spine of mountains from Costa Rica to Colombia forms the Continental Divide, largely separating the isthmus into the Caribbean and Pacific sides. This chain of hills and mountains greatly influences precipitation, with rainfall being far higher on the Caribbean side creating a distinct distribution of habitats, with humid tropical forest primarily on the Caribbean side and dry forest on the Pacific side. LP-EH archaeological contexts are restricted to the Pacific side of the Continental divide [46]. Sea level reconstruction from the Late Pleistocene suggests the Pacific coastal plain extended a further 80 km, with hypothesized temperature and precipitation favoring a thorny shrub landscape [47]. Lithic assemblages recovered from LP-EH contexts in Panama including Clovis, waisted Clovis, and fishtail points indicate the importance of hunting as a subsistence activity, with similar toolkits used in North and South American contexts being associated with a range of faunal remains, from small mammals to now-extinct megafauna [46,48]. Arrowroot (*Maranta arundinacea*), squash (*Cucurbita moschata*), and lerén (*Calathea allouia*) appear in the phytolith record by 8 ka BP [49]. Later evidence demonstrates the transfer of specific knowledge and technology between Central and South America in both directions, with important crops, lithic technology, and genetic human populations moving in both directions [48,50–52]. Further research is needed to confirm the routes early migrants took and what ecosystems they transited through, what ecological knowledge was developed, and how this influenced migratory and subsistence choices. The transfer of knowledge of plant taxa encountered in the various environments of Central America into the environments of South America will be fundamental to understanding these decisions. Furthermore, better understanding of the timing and routes of migration across the various habitats will facilitate the questioning of the longevity of ecological knowledge and whether it requires immediate application or can be passed through successive generations.

Upon entering South America, a diversity of landscapes would have been presented to the new arrivals. Coasts, savannas, humid lowland forest and the rising Andes provide distinct landscape choices for migrating settlers. Colombia can be broadly divided into five biogeographical regions: (i) Pacific, (ii) Caribbean, (iii) Andean, (iv) Orinoco, and (v) Amazon (Figure 1), with each characterized by distinct ecosystems. The Pacific Region, encompassing the biogeographic Chocó, stretches along the western coast from the Gulf of Uraba to Ecuador, and bordered to the east by the Western Cordillera [53]. The region is one of the wettest lowlands on the planet, receiving >7500 mm of rain a year [54]. Thick rainforests cover most of the landscape, with patches of mangroves along the coastal margin [55,56].

Figure 1. Map showing the location of key sites mentioned in the text and the five biogeographic zones of Colombia: Caribbean, Pacific, Andean, Orinoco, and Amazon.

Today, the region is sparsely populated and many areas are inaccessible, preserving the highly diverse rainforest. Palaeoecological, climatological, and archaeological data from the region are severely limited. Modern forest inventories document highly diverse vegetation [57]. However, long vegetation histories consist solely of one sediment record from Laguna Piusbi [55], which dates from 7670 yr BP but only has abundant pollen from 4400 yr BP, and one 4200 year record from Lake Jotaordó [58]. Although palaeoecological reconstruction is lacking for the LP-EH, the extreme rainfall of the region would have allowed a substantial reduction in precipitation before any ecological threshold is met and broad ecosystem changes are felt. Thus, hyper-humid forests are predicted to have dominated the landscape since the LGM. Archaeological data are absent for this early period. Inaccessibility and a climate unfavorable to preservation have limited the amount of research and the recovery of archaeological materials, which was potentially an appealing migratory route for early colonists. The combination of coastal and terrestrial resources are an attractive option and, although the high precipitation poses challenges, the stability and reliability of the climate could facilitate dependable subsistence strategies. The presence of well-established settlements at Monte Verde in Southern Chile ca. 14,000 cal BP, with evidence of extensive marine resource exploitation [59], perhaps hints toward a rapid southward migration along the Pacific coast. Future research is required to explore this region for its early human history, its potential as a corridor for human expansion further south, and the relationships between early humans and plant resources.

To the east of the Darien is the Caribbean region. The region is largely composed of low-lying savannas, including the Llanos Orientales, but also includes the Sierra Nevada de Santa Marta mountain range and the Guajira Desert. Vegetation across the Llanos Orientales varies from treeless savanna grasslands to savanna-woodlands with up to 80% tree cover [60–62]. A number of pollen records have been published from lake cores across the Llanos Orientales [61,63–65] with dry herbaceous vegetation dominating the landscape between 20–7 ka BP. The pollen record of Laguna El Pinal [65] records 85–92% *Poaceae* between ca. 22,400–12,500 ka BP. Shrub and tree taxa account for just 5% of the pollen from this period, rising to around 15% by ca. 10,300 ka BP. Trees and shrubs are particularly represented by gallery forest taxa, including *Mauritia*-type, *Alchornea*, Arecaceae, *Cecropia*, Melastomataceae, Myrtaceae, and *Celtis*. An absence of aquatic taxa suggests a dry environment and the seasonal drying of the lake [65]. *Mauritia* and *Mauritiella* palms are present in the Lake Sardinas record from ca. 12,300 ka BP [63]. Archaeological data for the Llanos Orientales is absent for the LP-EH, although the Taima-taima site in Venezuela provides a record of early human hunting activity [19]. The megafauna kill site includes El Jobo lithic artefacts in direct association with butchered mastodon (*Haplomastodon*) remains dated to ca. 13,000 years ago [8]. The Caribbean region no doubt formed an essential corridor in the migration of early settlers, especially exploiting the medium to large fauna on the savannas. Future research will hopefully determine whether, and to what extent, there was a human presence in the Llanos Orientales during the early human expansion across South America.

The Andean region is highly heterogeneous, encompassing three cordilleras with high elevation plateaus, intermontane valleys, and a diversity of ecosystems and climate regimes [66–70]. Elevation rises from the valley floors to a high point of 5755 masl. Elevation and aspect greatly impact land cover, with climate change throughout the Holocene causing shifts in the altitudinal distribution of vegetation zones. Below the frozen mountain peaks, grass páramo (above the treeline) currently occupies the zone between 3900–4600 m. Andean and sub-Andean forests constitute the main forest biomes at lower altitudes, with a mix of dry forest and savanna grasslands present depending on edaphic conditions and local climate regime.

2.2. Archaeological Setting

The earliest potential evidence of humans in northwest South America comes from the Pubenza site in the Middle Magdalena inter-Andean valley, where possible unifacial tools associated with mastodon remains (*Haplomastodon waringi*) date to between 19.9 and 16.2 ka BP within a likely seasonal tropical forest context [71,72]. Further research is required to confirm the anthropogenic component of the context and the human-plant relationships. The earliest secure human evidence in Colombia is presently from contexts on the high plain of Bogotá (ca. 2600 masl). These sites are associated with a lithic industry known as the Abriense or edged tool tradition [73]. Secure Late Pleistocene contexts are recorded at the Tibitó site, dating to ca. 13,600 ka BP [74], the Tequendama rock shelter, dating to ca. 12,850 ka BP [20], and El Abra. Excavations at El Abra II site produced a date of ca. 15,236 cal BP, although the anthropogenic nature of the context has been contested [71,75,76]. Secure human contexts at El Abra, recently excavated by this manuscript's authors, contain lithic artefacts and charcoal on a use-surface dating to ca. 12.5 ka BP (Report on file with ICANH). The open air Tibitó site is a butchering site where remains of mastodon (*Haplomastodon* sp. and *Cuvieronius* sp.), American horse (*Equus* sp.) and deer (*Odocoileus virginianus*) were recovered in association with Abriense tools and charcoal [77]. Abriense lithics are made by direct percussion to extract flakes without platform preparation [22,73,75]. Flakes are then retouched with direct percussion and are therefore considered in the edge-trimmed tool tradition [20,75]. The lithic industry at the Tequendama rock shelters, dating to ~12.5 ka BP and called Tequendamiense, differs from the Abriense tradition, featuring the use of allochthonous materials, a projectile point fragment, scrapers, and thinning flakes from exotic raw materials [68]. Technologically, the bifacial thinning is the key difference between Tequendamiense and Abriense lithics [73]. Located within cool páramo dwarf forest and open grassland in the Bogotá high Andean plateau, the lithics were recovered in association with brocket deer (*Mazama americana*), white-tail deer (*Odocoileus virginianus*), and rodents (Cricetidae).

The Middle Cauca, in the inter-Andean valley between the western and central cordilleras, has one of the richest LP-EH human records, starting at ca. 12.6 ka BP. The archaeological assemblage of the Early Holocene includes a range of lithic technologies including projectile points [73,78], unifacial flake tools made from local raw materials (andesite, basalt, dacite, quartz), as well as a few examples of plant processing tools, including handstones, a flat milling stone, and adzes. Early plant exploitation is revealed in the archaeobotanical record, including remains of *Xanthosoma*, Fabaceae and *Dioscorea* among others [21,79]. Contexts in the sub-Andean forests around Calima report similar findings [80].

In the Upper Cauca River Basin, in the sub-Andean forest around Popayan at 1600 masl, the site of San Isidro dates from ca. 10 ka BP. A diverse lithic assemblage accompanies the site, including thousands of flaked chert and obsidian artefacts, bifaces, projectile preforms, and retouched flakes. The assemblage also includes edge ground cobbles, flat milling stones, cobbles with concave groves, and a ground stone axe [80]. The archaeobotanical record at San Isidro includes seeds of avocado (*Persea* cf. *americana*), basul (*Erythrina* cf. *edulis*), *Caryocar* spp., *Virola* spp., and palm macro remains, likely belonging to *Acrocomia* [7,80]. Starch grain analysis from an edge ground cobble identified cf. *Xanthosoma/Ipomoea* and/or *Manihot* and *Maranta* cf. *arundinacea*, and non-identified grasses and legumes [7]. The mix of fruit trees and tubers in the record suggest a form of agroecology was being practiced by 10 ka BP [16].

The low-lying Amazon region to the east of the Eastern Cordillera comprises both savanna and humid tropical forest. The Caquetá and Guaviare Rivers dominate the area. The Peña Roja site along the Caquetá River and the archaeological sites of the SLL, focused on in this paper, are the earliest dated sites for the region and provide the limited archaeobotanical evidence of plant use. Peña Roja, with initial occupation dated between ca. 11,069 and 9168 cal BP [17,23,81,82], includes a lithic assemblage comprised of hand stones, milling stones, drills, choppers, hammerstones, hoes, and unifacial flakes, all of which are manufactured on local chert, quartz and igneous stone [81]. A diversity of palms and edible fruit trees are represented in the macrobotanical assemblage [82,83], including: *Anaueria brasiliensis*, *Astrocaryum aculeatum*, *Astrocaryum chambira*, *Astrocaryum jauari*, *Bactris* sp., *Euterpe precatoria*, *Oenocarpus bacaba*, *O. bataua*, *O. minor*, *Mauritia flexuosa*, *Parkia multijuga*, *Inga* spp., *Passiflora quadrangularis*, *Brosimum guianense*, *Sacoglottis* spp. and *Caryocar* spp. [82,83]. Phytoliths from squash (*Cucurbita* spp.), bottle gourd (*Lagenaria siceraria*) and leren (*Calathea* sp.) [7], and starch grains of *Xanthosoma* spp. on two stone tools dating from ca. 8.8 ka BP [82], are also documented.

Excavations in Serranía de Chiribiquete, 160 km to the south of SLL, record 36 rock shelters, with rock paintings similar to those at SLL. Radiocarbon dating of a hearth feature at Arc 1 rock shelter, which included ochre fragments and faunal remains, provided a date of ~5.5 ka BP [84]. Similarity in artistic expression to the SLL suggests cultural interaction between the two areas and earlier contexts, contemporary with the early dates of SLL and highly likely.

2.3. Study Region

The SLL, in the Department of Guaviare, is a 20 km^2 series of rocky outcrops along the Guaviare River on the ecotone between savannas and the Amazon rainforest [85]. Today's climate is warm and humid, with ~2800 mm annual precipitation. The climate is seasonal with a dry season from November to February and a wet season from March to October [86]. Palaeoenvironmental reconstructions are lacking for the region. The closest pollen record is the Loma Linda lake [87], 150 km to the north, which presents the area as savanna with gallery forest since ca. 9.6 ka BP. Piperno and Pearsall [7] extrapolated from existent pollen records to suggest that areas that host tropical forests in the region today were savannas at the end of the Pleistocene. However, recent combined palaeoclimate and palaeoecological data show that during the driest climatic events of the Late Pleistocene, even the driest parts of Amazonia (such as the 'dry corridor') continued to host tropical forests [88]. More localized paleoenvironmental records will help to calibrate these reconstructions.

The archaeobotanical records from SLL [18] and Pena Roja [17,82], attest to the presence of tropical rainforest vegetation alongside savanna taxa during the LP. A diversity of palms, the monocots *Heliconia* and *Phenakospernum*, and tree species such as *Brosimum lactescens*, a dominant tree species of the *terra firme* forest [89], confirm the presence of tropical rainforest elements, alongside the savanna grasses. Compared to today's environment, the landscape likely incorporated more open, patchy forest with species composition reflecting the lower precipitation and cooler temperatures of the LP. Recent plant inventories record 884 species of vascular plants, corresponding to trees, shrubs, vines, herbaceous plants and palms. Trees and shrubs are smaller where sediments are shallow on the rocky substrate [85,86]. There are a total of 449 vertebrate species, including fish (89), amphibians (30), reptiles (56), birds (226), and mammals (48), including monkey, armadillo, tapir, agouti, opossum, and anteater [85].

The SLL is composed of cretaceous sedimentary rock of the Araracuara formation, forming extensive rock shelters and rock faces that have been decorated with pictographs [18,90,91]. Excavations were first conducted in SLL during 1989 at the Angosturas II rock shelter. Lithic artefacts, charred botanical remains, faunal bones and ochre fragments were recovered, dating between ca. 8155 and 3977 cal BP [83]. Recent surveys and excavations in the region have documented many more painted rock shelters and established LP contexts (ca. 12.5 ka BP) in three separate rock shelters [18].

Cerro Azul is a distinct rock outcrop (Figure 2) and local landmark (322 masl, 2°31′47.2″ N and 72°51′59.0″ W). The most extensive excavations in the area have been conducted at the outcrop, which contains one of the largest sets of rock paintings in the region (Figure 2), with a total of 12 panels and thousands of images depicting humans, animals, plants, handprints and geometric shapes [18]. Archaeobotanical, lithic, and zooarchaeological analyses were conducted on the excavated material, which are reported in detail in Morcote-Rios et al. [18]. Here we revisit the methods and results of the analyses to aid further discussion.

Figure 2. (**a**) Aerial photograph of the prominent Cerro Azul outcrop; (**b**) Painted panel of rock art at Cerro Azul.

3. Materials and Methods

A 12 m^2 excavation was undertaken in 2017 following cultural stratigraphy. All removed sediment was screened to collect artefacts and ecofacts. Macrobotanical and faunal analyses were conducted on all recovered material in arbitrary 5 cm levels to maintain higher resolution vertical control, following standard procedures [92]. Phytolith samples were collected from a column in the excavation unit wall following completion of the excavation. Phytoliths were analyzed following standard protocols [93] and comparison to the phytolith reference collection at the Laboratory of Archaeology of the Natural Sciences Institute of the Universidad Nacional de Colombia (ICN-MHN-FIT) and phytolith atlases [94]. Each sample was based on a 200 count. Charcoal samples were collected for AMS radiocarbon dating to establish the timing of the initial occupation.

4. Results

4.1. Chronology

Excavations revealed an intact stratigraphy (Figure 3) and a secure date of human occupation from 12,180–11,826 cal BP. Two lower AMS dates, ca. 20 ka BP, cannot be confirmed as anthropogenic at present [18].

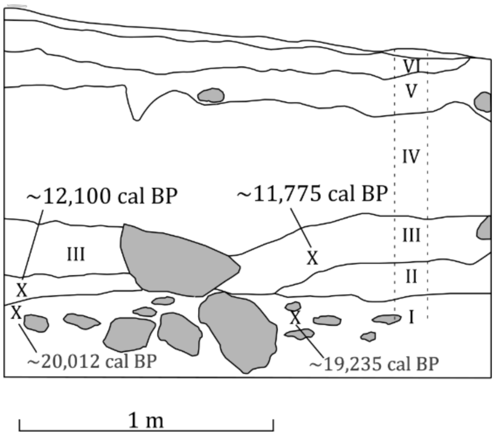

Figure 3. Stratigraphic profile of Excavation 1 from Cerro Azul showing strata (strata labeled with Roman numerals) and AMS radiocarbon dates. Dashed lines indicate the sampling column for phytolith analysis. For full profile drawing and description see Morcote-Rios et al. [18].

4.2. Lithics

Lithic artefacts of chert and quartz were recovered from all cultural strata at Cerro Azul. In total, 2478 pieces of manufacturing debris, 289 identifiable tools, and 128 cores were recovered. No polished lithics were recovered. The assemblage includes small unifacial tools of chert (216), quartz (48), and quartzite and sandstone (25), including examples of use-wear and micro-serrations along the edges. Cores have an average length of 60 mm, matching the size of the natural nodules on the landscape today. Abundant chert and quartz cores along the Guayabero River rarely exceed 100 mm length, suggesting the availability of natural resources limited the potential size of manufactured tools. Broadly, the lithic technology of Cerro Azul is part of the tradition of unifacial forms and expedient tools found across the Late Pleistocene across many South American regions, with similarities to the Abriense technology identified from LP contexts on the Bogota Plateau. There is no evidence of technological change in the lithic assemblage through the cultural sequence.

4.3. Plant Remains

Archaeobotanical analyses were conducted on carbonized seeds, plant charcoal, and phytoliths. Wet and dry screening at Cerro Azul recovered 32,489 carbonized seeds across the stratigraphic profile (Figure 4). Monocots are particularly well represented. Palm (Arecaceae) is the most represented family with ten taxa identified: *Astrocaryum chambira* (vernacular name [95–97] in Colombia: chambira, cumare, in Brazil: tucuma), *Attalea maripa* (CO: palma real, inaya, BR: inajai), *Attalea racemose* (CO: coco, BR: babassu), *Attalea* sp., *Bactris* sp., *Euterpe precatoria* (CO: asai, guasaì, BR: açaì), *Mauritia flexuosa* (CO: moriche, canangucho, BR: buriti), *Oenocarpus bataua* (CO: milpesos, seje, BR: batauà), *Oenocarpus minor* (CO: milpesillo, vacaba, BR: bacaba), and *Syagrus orinocensis* (CO: churrubay, coconut). Poor preservation (too fragmented, morphological features distorted) precluded taxonomic identification beyond the family. Morphological features of these remains are suggestive of the subfamily Arecoideae (possible genera: *Astrocaryum*, *Bactris* or *Syagrus*).

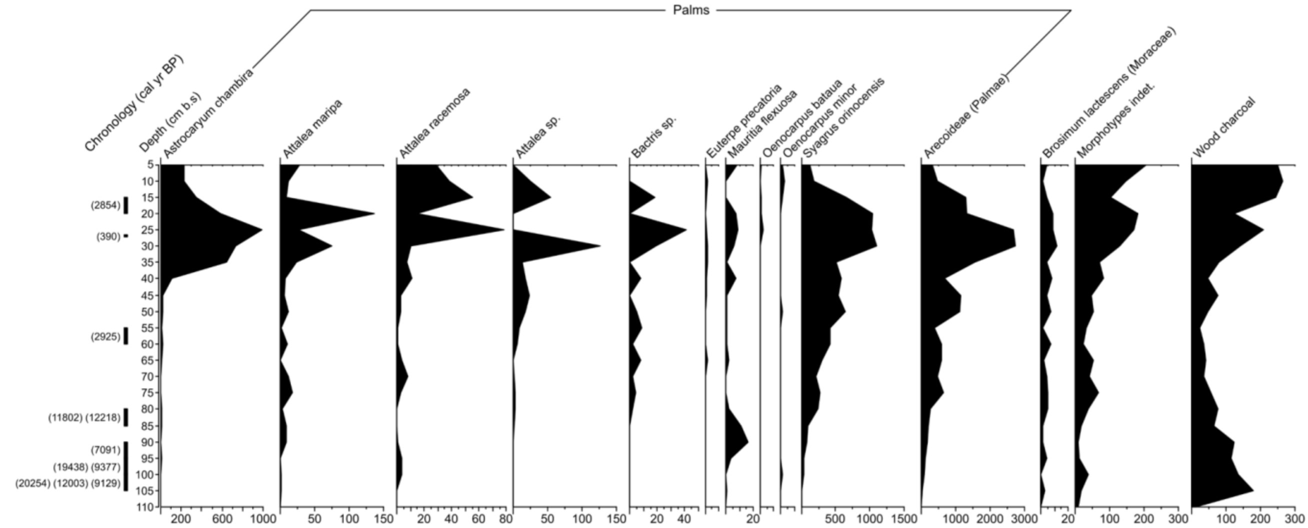

Figure 4. Diagram of macrobotanical remains from Excavation Unit 1 from Cerro Azul. Macrobotanical remains were analyzed from arbitrary 5 cm levels collected during excavation. Data are presented by depth below surface. Reprinted from Morcote-Rios et al. [18], with permission from Elsevier.

Syagrus orinocensis, *Astrocaryum chambira*, *A. maripa* and *A. racemose* have the highest representation, while *Euterpe precatoria*, *Mauritia flexuosa*, *Oenocarpus bataua* and *O. minor* are present in lower quantities. Carbonized macro remains of *Brosimum lactescens* (Moraceae) are present in all strata, indicating its continued use as an edible. Seeds belonging to the families Araceae, Euphorbiaceae, Humiriaceae, and Poaceae are associated with more research human activity in the upper stratigraphy. A total of 2388 fragments of woody charcoal were also recovered, likely representing various domestic activities at the rock shelter, including heat generation and food preparation. Fragments corresponding to palm trunks may indicate their use as fuel.

The palm family is also the best represented in the phytolith assemblage (Figure 5). *Mauritia flexuosa* and the groups *Astrocaryum-Bactris*, *Euterpe-Oenocarpus*, as well as other palmae indet. (globular echinate) category, being the most abundant. Trapezoidal, rectangular, bilobate phytoliths, and bulliform cells, diagnostic of grasses, indicate open areas were present in close proximity to the site.

Other identified taxa of note in the phytolith assemblage include *Heliconia* sp. Edible rhizomes of *Heliconia hirsute* are still consumed in the Amazon, while leaves of *H. hirsuta* are used in the construction of baskets. Phytoliths of the multi-purpose *Phenakospermum guyannense* (Strelitziaceae) were also recovered. The seeds of the species are edible and its leaves are used in campsite construction by the modern Nukak [86,98,99]. Phytoliths from arboreal and herbaceous dicots are present throughout the archaeological sequence (indet. morphotypes). Unfortunately, these groups do not produce diagnostic morphotypes to allow greater taxonomic resolution.

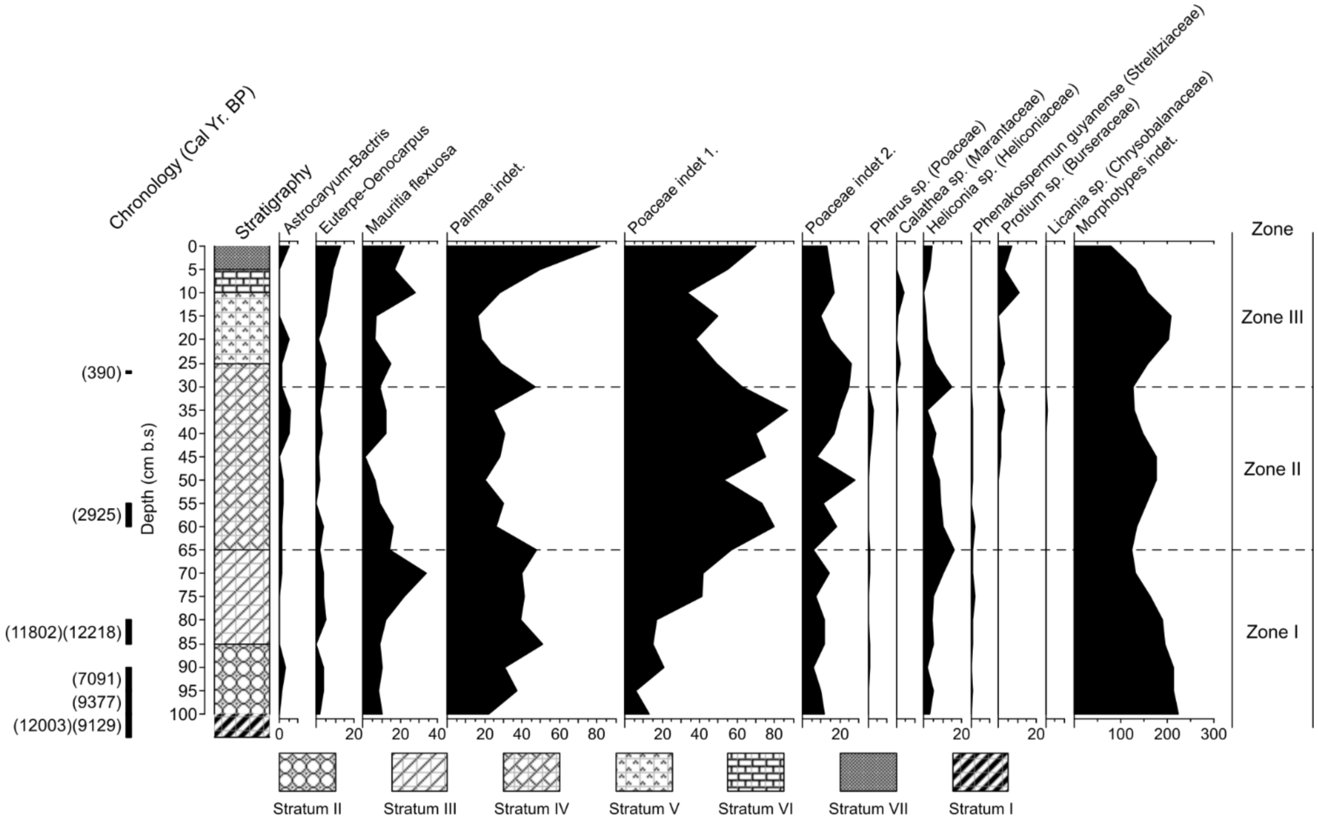

Figure 5. Phytolith diagram from Excavation Unit 1 from Cerro Azul. Reprinted from Morcote-Rios et al. [18], with permission from Elsevier.

4.4. Faunal Remains

A total of 81,669 faunal fragments were analyzed from the Cerro Azul excavation, 14,594 (18%) of which are diagnostic and 67,075 (82%) are non-diagnostic. The assemblage includes fish, mammals, reptiles, a small number of bivalves, and a single bird bone. Fish are the most abundant, accounting for 58% (8484) of the assemblage. The most abundant is cachama (*Piaractus* sp.), a species that migrates along rivers, entering seasonally flooded areas and lakes during the fruiting season of many arboreal forest taxa. Piranha (*Pygocentrus* sp.), which inhabit flooded grassy areas along river banks, lakes and streams [100], Cynodontidae (dogtooth characins), carnivorous predators found in rivers and seasonally flooded lakes, and Doradidae (catfish), which inhabit slow-moving rivers and lakes [100,101], are also represented.

Mammal remains (4930) account for 34% of the faunal assemblage. Bone plates from the shell of *Dasypus* (armadillo), which inhabits a range of habitats including tropical forest and open savanna, comprise 89% of the assemblage. Rodents are also well represented (5.37%), the most abundant species being the paca (*Cuniculus paca*) and capybara (*Hydrochoerus hydrochaeris*), both of which inhabit forests and savannas, where they feed on seeds, fruits, and tubers [102]. Cervideae (deer) account for 1.8%.

Reptiles, including caiman, crocodiles, iguanas, snakes, and turtles, account for 6% of the assemblage (824 fragments). These species are mostly associated with aquatic environments in the humid tropical forest [103]. A single phalange fragment from an egret (family Ardeidae), associated with rapids and wetlands, is the only bird bone in the assemblage. Bivalves of the family Mycetopodidae represent 2% (326) of the assemblage. These bivalves are most abundant and easy to harvest when water levels are at their lowest [104].

The complete assemblage is characterized by the exploitation of a broad spectrum of faunal resources, with a focus on those associated with aquatic environments. This focus is further emphasized when considering the absence of medium- and large-sized mammals, such as peccary (Tayassuidae), tapir (Tapiridae), primates, carnivores and birds. If the Cerro Azul occupants hunted and consumed larger animals, they were processed at a different site, with only small animals processed in the rock shelter. Similar proportions of faunal remains amongst fish, mammals and reptiles were maintained throughout the occupation history of the site, revealing a continuity in hunting subsistence practices.

5. Discussion

Jones discussed the importance of key visual traits in plant communities that enabled the transfer of ecological knowledge between different habitats, allowing successful foraging within a novel environment. He hypothesized as to how ecological knowledge transfer could overcome the increasing challenges of plant exploitation with hominin expansion into more northerly latitudes. Here we speculate that the same processes of ecological transfer and experimentation occurred in the reverse direction as humans migrated southward into the highly biodiverse humid tropical Amazon forests. We discuss the diet of these early settlers in the SLL, their dietary choices that enabled them to establish themselves in the region, and the potential application of ecological knowledge in subsistence choices. In particular, we focus on the dominance of palms within the archaeobotanical assemblage and suggest the plant family provided a “gateway” to the diverse tropical forest.

5.1. Diet

Faunal and botanical remains from Cerro Azul suggest the earliest settlers had a broad spectrum diet focused on hunting and fishing for their primary subsistence with plant gathering supplementing the diet. The hunter-gatherers of SLL used a broad range of animal resources. No large mammals were recovered in the assemblage, but diverse strategies and technologies would have been required for the capture and processing of the faunal resources, which include fish, small vertebrates, and mollusks [18]. Despite these hunting skills, there is limited lithic technological change and the exploitation of the various faunal resources was consistent throughout the history of the site (i.e., there are similar proportions of fish, mammals and reptiles throughout the stratigraphic sequence). The lithic assemblage of Cerro Azul is composed of unifacial and expedient tools, with an absence of bifacial forms or stemmed points. An absence of specialized plant processing tools suggests there was limited development of intensive plant processing. In particular, the absence of grinding stones suggests either the use of perishable technology or that roots and tubers were not as important as in other regions, such as the inter-Andean valleys [15], and sufficient plant foods could be efficiently procured without the need for more intensive labor investment, technological developments or processing experimentation. An interesting feature in the case of the SLL archaeobotanical record is that plant exploitation appears to have focused on a rather limited breadth of plant families, although further studies using specific methods that can pick up other plant remains (e.g., starch, parenchyma), could reveal a more complex diet. Tree fruits (e.g., *B. lactescens*) are represented, however, the assemblage is dominated by the palm family.

5.2. Palms

Ten palm taxa are identified in the assemblage at Cerro Azul: *Astrocaryum chambira*, *Attalea maripa*, *Attalea racemosa*, *Attalea* sp., *Bactris* sp., *Euterpe precatoria*, *Mauritia flexuosa*, *Oenocarpus bataua*, *O.minor*, and *Syagrus orinocensis*, and the dominance and diversity of palms in the archaeobotanical assemblage demonstrates that the plant family was specifically targeted as a resource. The focus on palm taxa may have provided a low risk, high potential foraging strategy within the biodiverse tropical rainforest.

Palms are one of the dominant plant groups on the landscape of the SLL today, growing in humid tropical forests, seasonally flooded, and flooded forests. Some species, such as *A. maripa* and *M. flexuosa*, form large populations. The palm taxa in the Cerro Azul assemblage are characterized as having a productive phenology with high productivity of fruits, seeds rich in protein and oils, and a fruiting period of several months of the year [105]. The leaves of various palm species are used for the thatching of homes and temporary campsites, while their fibers are used for various implements. The trunks are used in construction or to make blowguns, bows and harpoons for hunting and fishing [96]. All the palm species identified in the Cerro Azul assemblage produce edible components, with many species being multiuse, producing desirable fibers, thatch, and oils [105]. *Attalea* and *Astrocaryum* produce edible seeds, oil, thatch, and fibers. Mauritia flexuosa is one of the most abundant, and useful, palms on the South American landscape. The fruit of *Mauritia* is edible but can also produce flour. *Oenocarpus bataua* is a tall, oil-producing palm and practically all parts of the tree are utilized [106,107]. A high diversity of species of *Oenocarpus* in the middle Caquetá River has been suggested to reflect the center of diversification of the genus and that humans may have had a significant role in its spread across the humid lowlands [105]. For the most part, harvesting and processing palm fruits does not require complex technology; although some species do require a degree of processing. For example, hot water is needed to soften the pulp of *O. bataua*, *E. precatoria*, and *M. flexuosa*, which are then macerated and passed through a colander.

Palm remains have been recovered from archaeological sites throughout the Americas, from the southern United States to southern Uruguay, with multiple genera and over 50 species recorded in archaeobotanical assemblages [105]. In Para State in the Eastern Amazon, palm macro remains were recovered from LP contexts at Caverna de Pedra Pintada [25], Gruta do Pequia [108], and Capela [109]. The LP sites Santana do Riacho [110,111] and Lapa do Boquete [27] in Minas Gerais contain remains of *Astrocaryum* and *Syagrus*. The LP/EH tropical mountain forest site of San Isidro in the interandean valley of Popayan [17], dated to 12,465–11,829 cal BP, contains an abundance of palm remains. Palm husks and seeds, potentially from the genus *Acrocomia*, were recovered. At the Peña Roja site in the Colombian Amazon, 60% of the macrobotanical assemblage corresponds to the palm family (Arecaceae) [17,83]. Identified palm taxa include: *Astrocaryum aculeatum*, *A. jauri*, *A. sciophilum*, *Attalea insignis*, *A. maripa*, *A. racemosa*, *Mauritia flexuosa*, *Oenocarpis bacaba*, *O. bataua*, and *O. mapora*. Palm continues to be one of the most important resources for present day communities in Amazonian forests [112–116]. The modern Nukak of Colombia, for example, manage eleven palm species (from seven genera) as a source of food or raw materials [83], with *Oenocarpus*, *Attalea*, *Bactis*, *Mauritia*, and *Astrocaryum* exploited for edibles [83,98].

5.3. Ecological Knowledge

The dominance and diversity of palm taxa in the SLL archaeobotanical assemblage is of particular interest when considering the application of ecological knowledge in a new environment. The various species of palm are instantly recognizable on the landscape, not just as monocots, but specifically to the Arecaceae family. Not only do the various palm taxa share a distinct morphology, but they also stand out as physically distinct from the wide variety of dicot trees that constitute the highly diverse forest vegetation. Their visual appearance is likely a key salient identifier of potential economic value, enabling the rapid development of a resource exploitation strategy and adaptation to the new environment.

The myriad uses of palm and the exploitation of the family by Amazonian groups is well documented [113,115,117,118] and archaeobotanical evidence from Late Pleistocene and Early Holocene archaeological contexts have been used as evidence to establish the role of palm as an important component of adaptive strategies in the humid tropical environment [17,105,119]. A question remains, however, over the behavioral process behind palm exploitation. Were palms a gateway species, enabling early resource identification in a novel environment? Did the settlers of the SLL transfer knowledge of palms from previous encounters in other landscapes, or was the knowledge developed through in situ experimentation? Assessing the potential behavioral process can provide insight into how new landscapes were colonized, with implications for short- and long-term human/plant dynamics and the global expansion of humans.

The palm family is present in a range of habitats across Central and South America. Palm species richness in Colombia is high relative to other countries in the Neotropics. Galeano and Bernal [96] record 231 palm species across 44 genera in present day Colombia. Only Brazil has more species (233), albeit across fewer genera (36). Ecuador is a distant third for species richness, with 134 species across 30 genera. The dynamic topography and location at the crossroads between Central and South America has created a mosaic of palm distribution in Colombia resulting in a great wealth of the taxa [96]. Galeano and Bernal [96] document 92 palm species in the Amazon (including the Llanos Orientales). The understorey taxa *Geonoma*, and spiny *Bactris* and *Astrocaryum* are particularly diverse, while the species *Attalea septuagenata*, *Oenocarpus circumtextus* and *O. makeru*, are exclusive to Colombia. Recent botanical survey by Balslev et al. [112] recorded a palm density of 2900 individuals per hectare in the *terra firme* Amazonian forest and a density of 3737 individuals per hectare in the floodplain forests. A total of 86 species are present in the Pacific lowlands (including the wet tropical forests of the Chocó), thirteen of which are exclusive to Colombia. The area has an incredibly high diversity for its relative size in comparison to the Amazon. The Andean region, including the Cauca and Magdalena valleys, includes 82 species. *Ceroxylon* is exclusive to the Andes and the genera *Wettinia* and *Aiphanes* are the most diverse. Galeano and Bernal [96] particularly drew attention to the endemic species of the Magdalena Valley, noting that while some of the lowland taxa are shared with the Amazon and Pacific regions, some are exclusive to the valley (especially in the genus *Astrocaryum*). The Caribbean region has the lowest palm diversity, with just 14 species. The dry region includes the genera *Sabal*, *Acoelorrhaphe*, and *Copernicia*.

Although Colombia benefits from extensive palaeoecological research, the records are far from complete for its highly diverse landscapes, and many areas lack LP-EH vegetation reconstructions. As such, the presence, distribution, and diversity of palms on the LP-EH landscape cannot be determined with a high-level of certainty at present. In their reconstructed biomes of the LP from existent pollen cores, Marchant et al. [67] principally associate palms with the Tropical Rainforest and Tropical Seasonal Forest biomes, which are geographically restricted to the Pacific and Amazonian regions. The Pantano de Monica 1 core [120] from the middle Caquetá River Basin in the central Colombian Amazon contains abundant Mauritia-type pollen from ca. 11 ka BP (extrapolated age), with low numbers of *Euterpe/Geonoma*-type also documented [120]. However, the diversity of palms in the region is best exemplified by the range of palm taxa recovered in the archaeobotanical assemblage at the Pena Roja archaeological site [17], which is further supported by the archaeobotanical assemblage from Cerro Azul.

In the other regions and biomes of LP Colombia, although there was a high diversity of endemic palm species, they were less abundant, occurring as scattered individuals or in small populations. Gallery forest, flood-plains, wetlands, alluvial soils, etc., would have provided suitable habitats for palms such as *Astrocaryum*, *Euterpe*, *Geomona*, *Mauritia*, *Mauritiella*, and *Oenocarpus*. The inter-Andean valleys likely contained a range of palm taxa. The records from the Cauca Valley suggest a heterogeneous landscape. Arecaceae pollen is present in low abundance in the Quilichao (1020 masl) and La Teta (1020 masl) sediment cores [66]. The pollen assemblage suggest the presence of dry forest during the LP [66], and palms may have been more restricted to the proximity of water bodies. The archaeobotanical assemblage at the San Isidro archaeological site (1690 masl), dated to 11,802–11,271 cal BP [7], includes palm macro remains most likely belonging to *Acrocomia* [17]. The assemblage at San Isidro suggests the presence of sub-Andean forest, similar to the tropical rainforest, albeit with fewer and less abundant species and no modern analogue [17].

A lack of LP-EH stratified archaeological sites or palaeoecological records in the Magdalena Valley prevents confirmation of palm taxa during the initial peopling of the region. The Laguna Pedro Palo pollen record [121] from 2000 masl on the western slopes of the Eastern Cordillera does not record any palm taxa during the LP-EH. Hooghiemstra and van der Hammen [121] note the present distribution of palm in the lowland tropical vegetation belt (0–1000 masl) of the valley, as well as a more limited occurrence into the sub-Andean forest belt (ca. 1000–2300 masl), although they acknowledge two types of sub-Andean forest, with the upper zone (above 2000 masl) characterized by *Quercus* forest with certain taxa, such as palm, not extending into the higher altitudes. During the LP-EH, the Magdalena Valley constituted the major forest refugia across all inter-Andean valleys. Such forest refugia would have contributed to the development of a diversity of endemic species, accounting for the high species richness of palms on the modern landscape in the valley. The archaeological site of El Prodigio on the eastern slope of the Central Cordillera (1800 masl) contains carbonized palm remains dated to ca. 6.4 ka BP [122]. Archaeological sites dated to ca. 10 ka BP in the Magdalena Valley are located in areas predicted to have hosted lowland tropical rain forest [123,124], which likely would have contained a variety of palms. Future archaeobotanical research at these sites would provide important information on plant usage as well as reconstructing the presence of specific taxa on the landscape.

In the savannas of the Llanos Orientales, pollen cores from Laguna Sardinas and Laguna Angel [63] record the presence of *Mauritia* palm as one of the principal tree species around water bodies during the LP. Archaeological data are presently absent for the region during the LP-EH. Any hunter-gatherer populations in the savannas would have had to rely on the permanent water bodies and as such would have been familiar with palm taxa.

The ubiquitous endemic occurrence of palm across the diverse habitats of Colombia, coupled with evidence of palm use in early archaeological sites, suggests the settlers of the SLL had likely previously encountered and developed knowledge of the economic potential of palms. Potentially, early migrants, or more likely their ancestors, may have encountered humid tropical forests in Central America, the Chocó, or isolated patches in the Andean valleys, on their journey to the Amazon. However, the spatial separation of the Amazon from other potential humid tropical forests, coupled with the present archaeological data that establishes humans in savanna and dry forest settings for over a millennia before the earliest humid forest contexts, strongly supports the humid tropical forest as a new environment for the pioneering settlers. Furthermore, any potential knowledge of the range of edible humid tropical forest taxa, either from direct previous experience or passed on from ancestors, does not seem to have been applied in Cerro Azul, as demonstrated by the focus on the single plant family. Upon encountering the vegetation of the Amazonian tropical forest, the distinct physical appearance of palm could have been a key salient marker that enabled the transfer of ecological knowledge through the rapid identification of potential edibles. Successful experimentation with fruits from one palm taxon would have likely facilitated further experimentation within the family. Thus, low risk experimentation built on the transfer of ecological knowledge can explain the noted human preference for palm as an adaptive strategy in newly encountered humid forests [17,125,126].

The ecotonal nature of the SLL region may have been particularly attractive for human colonizers, especially as pioneers first began to navigate the novel tropical forest environment. Hunter-gatherers could rely on established subsistence strategies, whilst new skills and knowledge were developed for the novel environment. Palms were clearly key taxa in early subsistence strategies in the region, providing a gateway to the tropical forest vegetation, while hunting and fishing provided a substantial contribution to the diet, particularly in the form of protein. This strategy could overcome the challenges that have been posited as being a barrier for securing plant foods in the tropical forest [30,31]. Through time, the reliance on plants could increase as knowledge and experimentation augmented and communities became more sedentary, with implications for the diversification, domestication, and spread of taxa across South America [105,127–129]. Although presently absent from the SLL, micro remains of *Cucurbita*, *Calathea*, and *Xanthosoma*, and ground stone plant processing tools, ca. 8.8 ka BP at Peña Roja [83], demonstrate a more diverse plant exploitation strategy employed in a tropical forest setting. The additive nature of ecological knowledge, in turn, could have facilitated further exploration, deeper into the tropical forest biome, increasing reliance on the tropical forest resources and initiating processes of plant and landscape domestication.

6. Conclusions

Evidence of plant use during the initial peopling of Amazonia is key to understanding early human ecology, hinting at strategies that allowed experimentation, risk management, and knowledge development. The diverse palm taxa recovered from Cerro Azul in the SLL on the ecotone boundary of the Colombian Amazon suggest this was a key plant family that enabled successful gathering in a novel tropical environment. The distinct physical appearance of palm, coupled with the economic importance of the family for edibles, construction material, fibers, and oil, could have facilitated the rapid identification of these economically useful plants amongst the diverse vegetation of the Amazon forest based on previously developed knowledge and low risk experimentation. The occurrence of palm taxa, in varying abundance and diversity, across the distinct environments of the Neotropics would have facilitated knowledge transfer and successful movement between habitats. The forefronting of botanical knowledge is likely an essential component of Pleistocene dispersals of Homo sapiens.

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