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Plant resource diversity in the ethnobotanical record of precolonial Puerto Rico: Evidence from microbotanical remains

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ABSTRACT

We present new starch grain and phytolith data from two sites in Puerto Rico: Maisabel and HU-7. Our findings reveal a strong emphasis on the use of maize, followed by chile pepper and arrowroot in Early and Late Ceramic Age deposits. Manioc was rare, with nearly all manioc residues coming from Early Ceramic Age artifacts in the Maisabel site. Integrating both starches and phytoliths provides a more accurate view of plant use than if only one or the other of these classes of microfossils are studied. We then review previously reported microbotanical findings from the island to document the diversity of plant resources utilized by precolonial occupants of Puerto Rico and how commonly these resources occur. There is now a sufficient body of residue data available to allow new insights into precolonial agricultural economies of Puerto Rico. Applying ecological measures of diversity, richness, and evenness to microbotanical datasets for Puerto Rico reveal declines in diversity for both the initial and later colonizing populations of the island. These findings are consistent with expectations from agroecology, whereby productive domesticates are identified and over time exploited in greater proportions to other taxa, both wild and domesticated.

1. Introduction

Micro and macrobotanical, zooarchaeological, paleoecological, and isotope studies conducted over the past several decades have greatly refined our understanding of West Indian precolonial and colonial survival strategies; social and economic relations; and movements of people, ideas, plant and animal species, and commodities. Prior to these studies, many of our assumptions regarding Ceramic Age or Neolithic lifeways and adaptive strategies were based on ethnohistoric and ethnographic accounts from the Caribbean and lowland South America (DeBoer, 1975; Lathrap, 1970; Sauer, 1966; Sturtevant, 1961) (Fig. 1). Broad distinctions in subsistence practices and associated social formations were made between the earliest Archaic (c. 5000–1000BC) and subsequent Ceramic Age (c. 500/700BC–Contact) colonizers to the West Indies (Rouse, 1992).

Based on limited evidence and many assumptions about early colonizers, Archaic groups were thought to be small, highly mobile bands of hunter-gatherers, foragers, fishers, and collectors (Rouse, 1992). The Archaic menu consisted of terrestrial and marine wild resources. In contrast, again based on some evidence and more assumptions, Ceramic Age colonizers to the West Indies were considered tribally based sedentary farmers derived from the Tropical Forest Culture of greater Amazonia (Lathrap, 1970: 45–67; Rouse, 1992).

The agricultural base of Tropical Forest Culture was dominated by root crops with a focus on manioc (*Manihot esculenta*) of the bitter variety, followed by sweet potato (*Ipomoea batatas*), yautía (*Xanthosoma*), New World yam (*Dioscorea trifida*), achira (*Canna edulis*), arrowroot (*Maranta arundinacea*), and jícama (*Pachyrhizus erosus*). Bitter manioc required elaborate processing to remove poisonous hydrocyanic acid (HCN) to make the tubers edible for humans. Processing entailed scraping the tubers, generally using a wooden board embedded with thousands of microflakes (grater board), to produce a wet mash or pulp and then expressing the HCN from the pulp with a basket squeezer (Fig. 2). After the pulp dried, it was sifted to produce flour that was then baked on a large ceramic griddle to make a large round bread (Yde, 1965: 28–51). Based on ethnographic observations of bitter manioc processing and bread production, archaeologists working in the Caribbean concluded that the presence of griddle sherds and microflakes was de facto evidence for manioc cultivation. Following DeBoer's (1975) early cautionary note about making such facile analogies to ethnographic Amazonia, numerous starch residue and microwear studies have now determined that griddles and microflakes do not necessarily

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indicate manioc use (Berman and Pearsall, 2000, 2008; Pagán-Jiménez, 2013; Perry, 2002, 2005).

In his starch residue analysis of 19 griddle sherds from Puerto Rico, Dominican Republic, and Cuba, Pagán-Jiménez (2013: 399) documented the presence of marunguey (*Zamia* sp., *Zamia amblyphyllidia*, *Zamia pumila*), sweet potato (*Ipomoea batatas*), maize (*Zea mays*), beans (Fabaceae, *Phaseolus vulgaris*), arrowroot (*Maranta arundinacea*), cocoyam (*Xanthosoma sagittifolium*), and annatto (*Bixa orellana*) in various combinations across those islands. Manioc starch was not found on these griddle fragments, which were collected from Late Saladoid (c. AD550–1000, Puerto Rico), Meillacoid (c. AD750–1350, Dominican Republic), and later Ostionoid (AD750–1450, Dominican Republic; AD1000–1350, Cuba; AD1250–1320, Puerto Rico) contexts (Pagán-Jiménez, 2013). Other earlier studies likewise failed to find evidence of manioc processing on stone grater board teeth examined for starch residues (Berman and Pearsall, 2008; Perry, 2005; Rodríguez Ramos and Pagán-Jiménez, 2006).

More recently, starch and phytolith residue analysis of artifacts from Early (c. AD700/800–1100) and Late (c. AD1100–1530) Lucayan sites in the Bahamas produced four chert microliths with manioc residues (Berman and Pearsall, 2020). In addition, these and other Lucayan artifacts yielded starch grains or phytoliths of *Calathea* (lerén, Marantaceae), Curcubitaceae (squash family), maize, and Arecaceae (palm family) (Berman and Pearsall, 2020). Nine griddle fragments from the c. AD1400 Palmetto Junction site on Providenciales of the Turks & Caicos Islands produced starch grains of manioc (30), maize (2), and zamia (2) (Ciofalo et al., 2019). Six limestone and two shell artifacts from the c. AD1100 Rolling Heads site, Long Island in The Bahamas produced starch grains of manioc (51), maize (17), and *Zamia* spp. (8) (Ciofalo et al., 2018). All these studies also listed unidentifiable taxa in their starch or phytolith results as did ours, discussed below. Finally, stable isotope analysis of 66 late precolonial Lucayan burials (c. AD1000–1600) suggests increasingly greater reliance on root crops in response to over-exploitation of marine resources (Schulting et al., 2021). In toto, the Lucayan data indicate that there may be distinctive local trends in subsistence strategies in response to specific challenges facing groups within subsets of the Caribbean islands.

Starch grain, phytolith, and paleoecological data from Puerto Rico and the Lesser Antilles also reveal land modification and horticultural activities dating to the Archaic (Burney et al., 1994; Pagán-Jiménez, 2013; Rivera-Collazo, 2015; Siegel et al., 2005, 2015). Pagán-Jiménez (2009, 2011a; Pagán-Jiménez et al., 2005) identified maize, cf. manioc, yautía, and batata starch grains on artifacts collected from three Archaic (pre-Saladoid) sites in Puerto Rico. Maize phytoliths were recovered from a sediment deposit underlying a depth dated to the Archaic in a core collected from a pond adjacent to the Maisabel site, Puerto Rico (c. cal 785BC) (Siegel et al., 2005: 111; Fig. 3). In Cuba, Chinique de Armas et al. (2015) identified starch grains in dental calculus of burials from the Canímar Abajo site dating to the Early (c. 1380–800BCE) and Late (c. AD360–950) Archaic periods. Starch grains included cultigens of beans (*Phaseolus vulgaris*/Early and Late Archaic) and possibly maize or batatas (*Zea mays* or *Ipomoea batatas*/Late Archaic). Botanical and paleoecological studies have conclusively determined that it is inappropriate to rely exclusively on ethnographic analogy or ethnohistoric accounts to interpret precolonial survival strategies in general and agricultural practices in particular. Collaborative research by Caribbeanists—

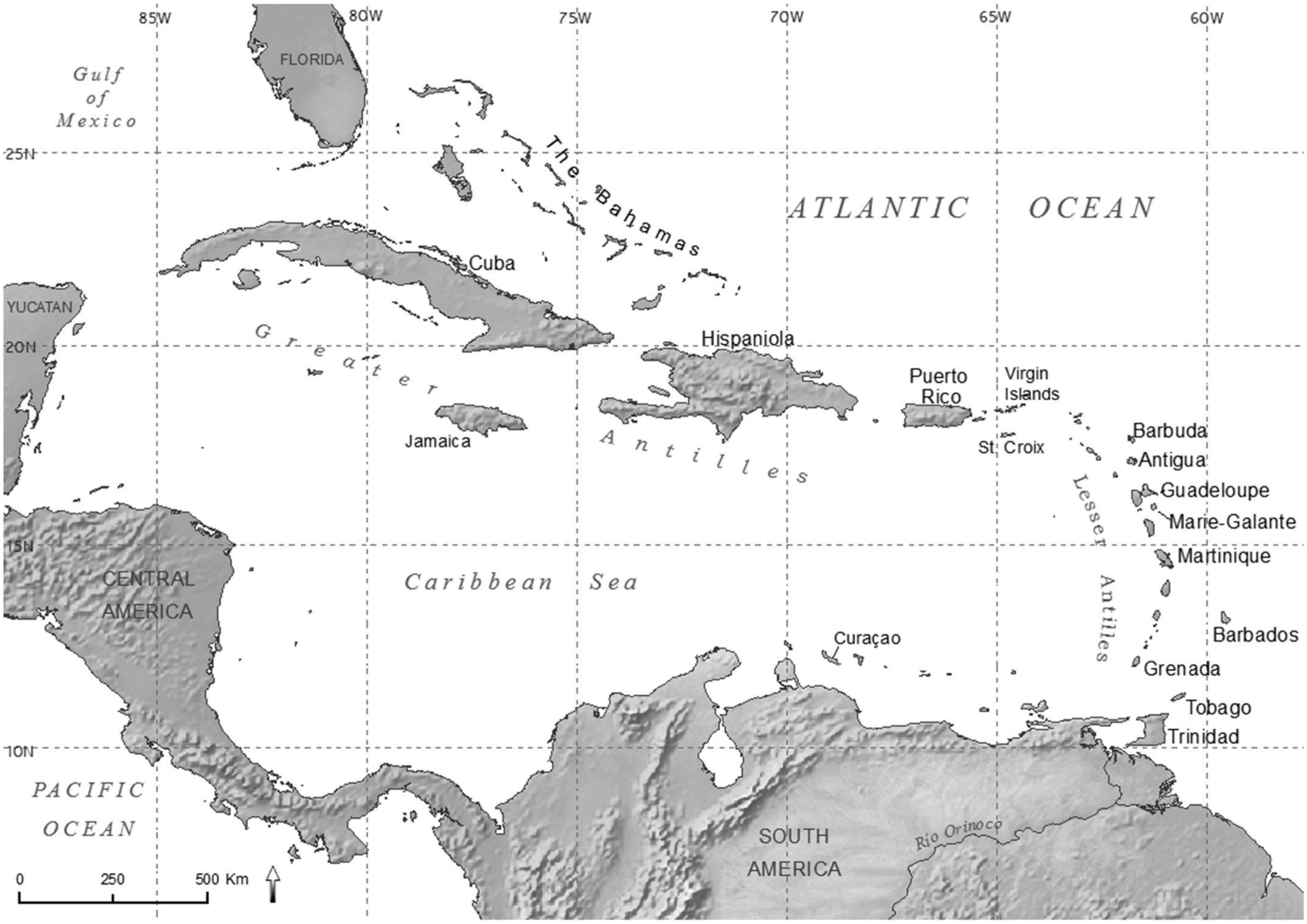


Fig. 1. Map of the Caribbean Basin.

archaeologists, paleoethnobotanists, and paleoecologists—has supported DeBoer's (1975) insights.

In this paper, we present new starch grain and phytolith data from two sites in Puerto Rico: Maisabel and HU-7 (Fig. 4). We then review previously reported microbotanical findings from the island to document the diversity of plant resources utilized by precolonial occupants of Puerto Rico and how commonly these resources occur. While more systematic studies are needed since sample numbers are often quite small there is a sufficient body of residue data available providing evidence into precolonial agricultural economies of Puerto Rico. Our review demonstrates that starch and phytolith studies of pottery, lithics, and teeth provide powerful insights into ethnobotanical practices and should be made a more central focus of research going forward. Further, additional research is needed into landscape-scale interactions through environmental coring to provide fine-grained contexts for site-based data (Rivera-Collazo, 2015).

At the current stage of microbotanical research in Puerto Rico, it is appropriate to explore ecological measures of diversity for comparing assemblages of taxa from sites regionally and through time. Ultimately, building a repository of local, regional, and pan-Caribbean diversity values will enhance our discussions of local or in situ developments in agricultural practices versus transported suites of domesticates, relative degrees of reliance on wild versus domestic plants, and geographic and temporal variability in survival strategies.

Our starch and phytolith findings from Maisabel and Site HU-7 reveal a strong emphasis on the use of maize, followed by chile pepper and arrowroot in Early and Late Ceramic Age deposits. Manioc was rare, with nearly all manioc residues coming from Early Ceramic Age artifacts in the Maisabel site. Integrating both starches and phytoliths provides a more accurate view of plant use than if only one or the other of these classes of microfossils are studied. Applying ecological measures of diversity, richness, and evenness to microbotanical datasets for Puerto Rico reveals declines in diversity for both the initial and later colonizing populations of the island. In addition, decreasing diversity in the microbotanical record through the Ceramic Age is linked to the formation of chiefly polities beginning c. AD600/700. These findings are consistent with expectations from agroecology, whereby productive domesticates are identified and over time exploited in greater proportions to other taxa, both wild and domesticated (Rindos, 1984).

2. The sites

Maisabel and HU-7 represent two very different kinds of sites. Maisabel was a large, intensively occupied settlement continuously inhabited from c. 340BC to AD1200, spanning the Saladoid and much of the Ostionoid periods. Located on the northcentral coast of Puerto Rico, it consists of five mounded middens arranged in an approximate circular pattern surrounding a centrally located cemetery (Siegel, 1995, 1996). At least one house area was identified between two of the mounded middens, represented by numerous features including postmolds, hearths, an earth oven, pits, burials, and a drainage ditch.

Maisabel artifacts sampled for residue analysis came from selected contexts in the two largest mounded middens. Teeth from six burials in the cemetery were studied separately (Mickleburgh and Pagán-Jiménez, 2012; Pagán-Jiménez and Mickleburgh, 2023). Except for five dated samples that underlay and predate cultural deposits and one that straddles the Cuevas and Monserrate complexes (Early/Late Ceramic Age), Mounded Midden 1 dates to the Hacienda Grande complex of the Early Ceramic Age Saladoid series (Table S1). Except for three historic-period dates, all the Mounded Midden 2 samples date to the Monserrate complex of the Late Ceramic Age Ostionoid series (Table S1). Rodríguez Ramos et al. (2023) recently proposed a revised chronology for precolonial Puerto Rico through Bayesian modeling of most available radiocarbon dates. The Maisabel dates were included in their study. The modeled calibrated ranges for the Maisabel dates changed insignificantly (compare Table S1 with Rodríguez Ramos et al., 2023: S1 Table).

Teeth from Maisabel Burials 2, 5, 14, 16, 17, and 21 were selected for starch-grain analysis (Mickleburgh and Pagán-Jiménez, 2012; Pagán-Jiménez and Mickleburgh, 2023). These burials date to the Early Ceramic Age or straddle the transition between the Early and Late Ceramic Ages (c. AD600–800).

HU-7 was a small Elenan Ostionoid village located along the east-central coast of the island. A 20 to 30-cm thick intact archaeological

Fig. 2. Grater board production and bitter manioc processing. Waiwai Indians in southern Guyana. The upper row of images shows the manufacture of grater boards. Lower left: three women grating manioc tubers in a recycled dugout canoe. Lower middle: expressing HCN from grated manioc mash. Lower right: sifting dried manioc mash into flour. Photographs by Peter E. Siegel.

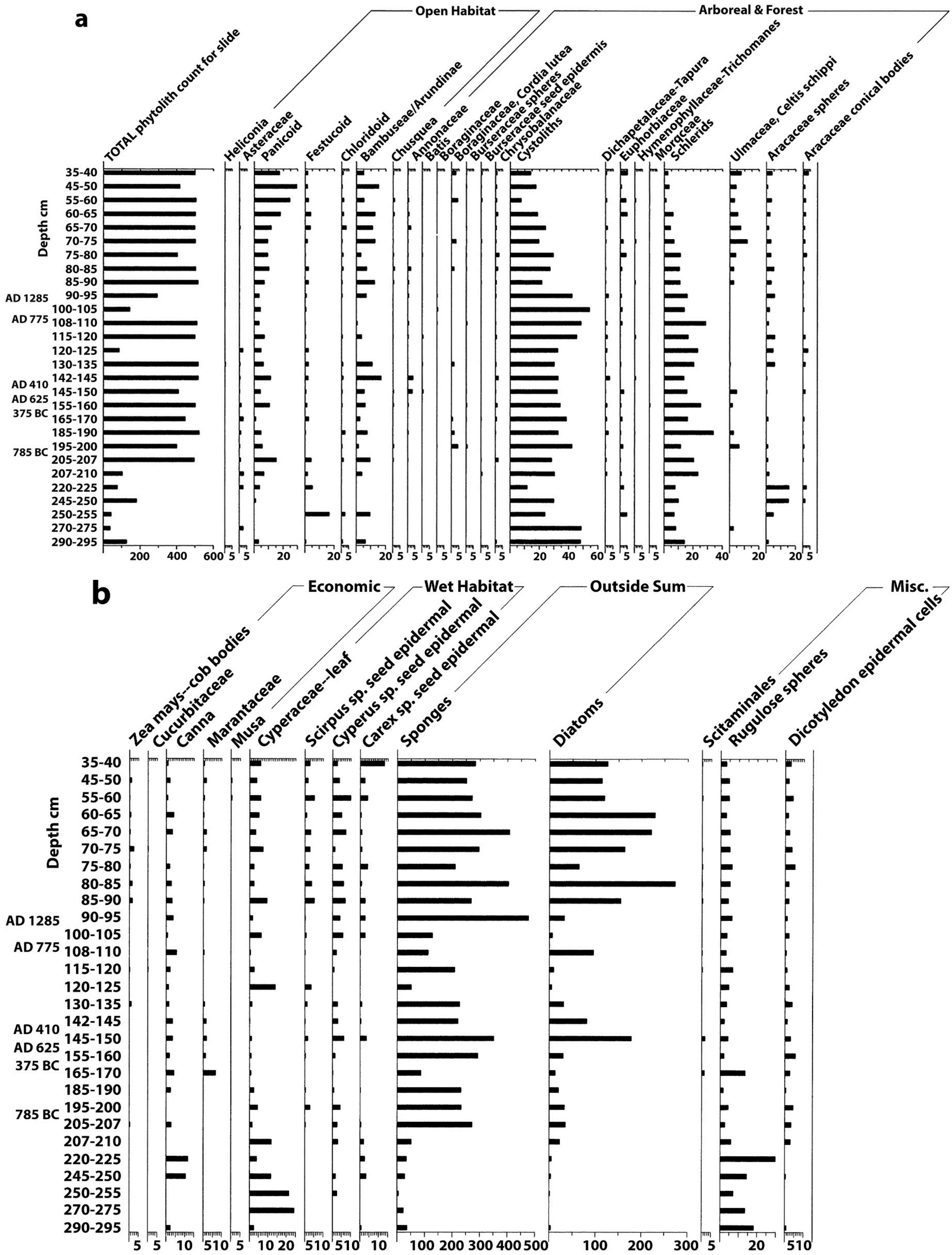


Fig. 3. Phytolith diagrams showing the plant taxa identified in the Maisabel pond core. Drawn using Tilia and Tilia graph (software by E. Grimm): (a) total phytolith counts and individual curves for open habitat and arboreal and other forest indicators, (b) economic plants, wet habitat indicators, phytoliths tallied outside the sum, and less useful types (misc.), (c) a composite diagram of the same data displays indicator subtotals. All curves are percentages, based on a 500-count, except when indicated. Note the occurrence of maize, especially below the c. cal 785BC dated sample.

deposit was buried beneath approximately 50 cm of historic alluvium (Siegel, 2002). The artifact assemblage consisted almost entirely of pottery with many large sherds that could be refitted to form nearly complete vessels. Aside from small, isolated shell, coral, and charcoal fragments, organic preservation was nonexistent thus radiocarbon dating of the deposit was not possible. Based on ceramic vessel

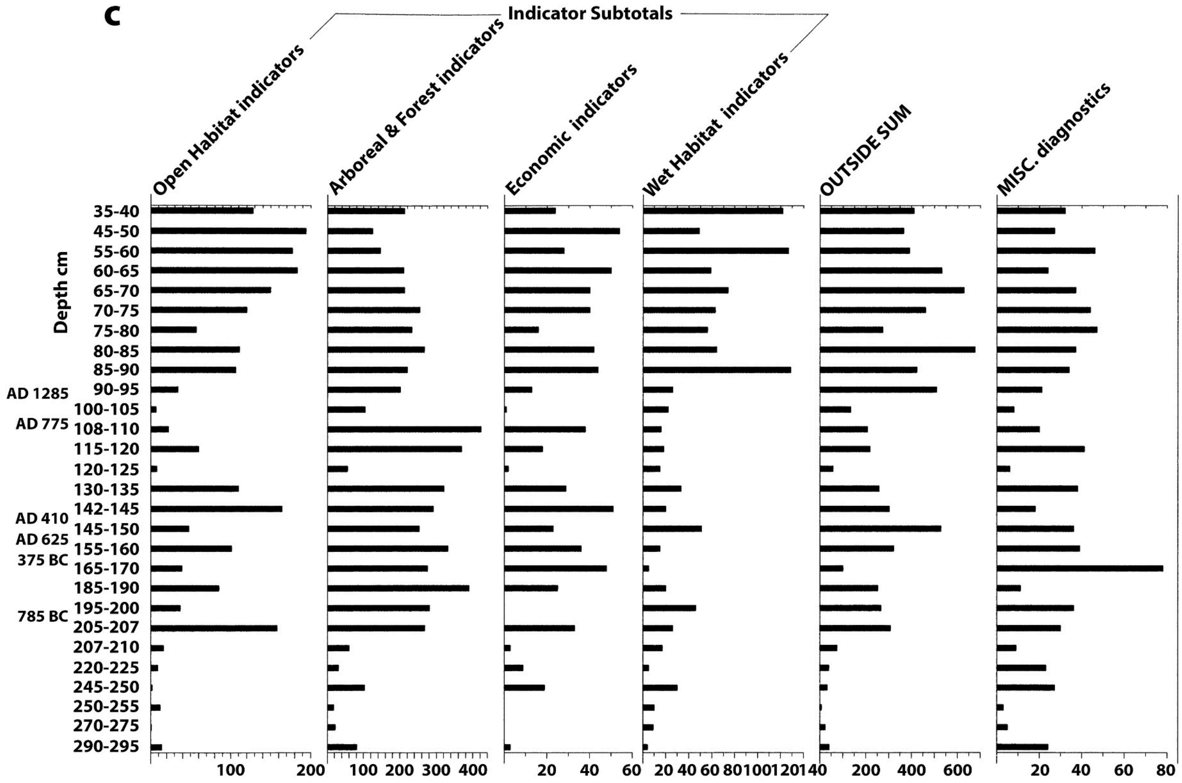


Fig. 3. (*continued*).

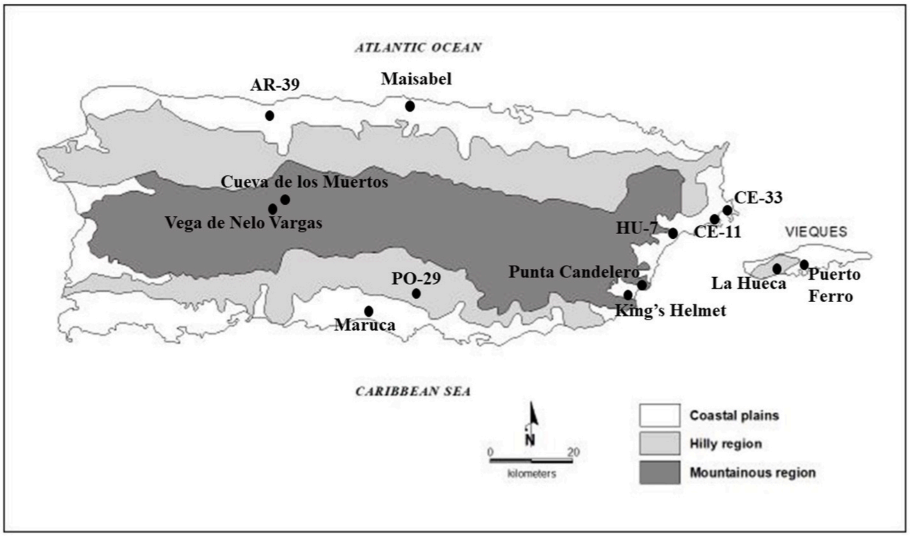


Fig. 4. Map of Puerto Rico showing the locations of sites discussed in the text.

reconstructions, vessel life history data, and spatial density distributions of artifacts, Site HU-7 represented a short 10 to 20-year occupation of at best a few households. Chronologically sensitive ceramics indicate that the site was occupied during the transition between the Monserrate and Santa Elena complexes (c. AD900–1000). Site HU-7 overlaps a portion of Maisabel's late occupation. Materials selected for study came from test units excavated in areas of the site with the greatest artifact densities.

3. Methods

3.1. Starch and phytolith preparation

In total, 28 artifacts were selected from the two sites for analysis (22 from Maisabel, 6 from HU-7) (Figs. S1–S7; Table S2). Each artifact was assigned two types of processing numbers, one for starch sediments (SS#) and one for phytolith sediments (PS#). Starch and phytolith grains were removed sequentially from samples, using the "piggy-back" processing procedure developed in the University of Missouri paleoethnobotany laboratory (Pearsall, 2015). Starches were collected first before subjecting samples to harsher chemicals used in phytolith extraction. Initially, three sub-samples, referred to as sediments, were created: Sediment 1, material removed by dry-brushing the artifact; Sediment 2, material removed by wet-brushing the artifact; and Sediment 3, material removed from the artifact by sonication. In this study, only one artifact, a griddle fragment from Maisabel (1.119.27), was sampled by dry-brushing (SS74) followed by wet-brushing and sonication. Since artifacts had been previously cleaned, the remaining artifacts were wet-brushed and sonicated only, producing Sediments 2 and 3. Starches and phytoliths were extracted from each of these sediments sequentially (Pearsall, 2015).

Following starch extraction, microscope slide-mounts were created for each sample by pipetting extract onto a slide and adding glycerin and a cover slip. Coverslips were sealed using nail polish. If no starch was observed in one microscope slide mount, this information was entered in the spreadsheet. In a few cases, a second slide was made and examined. Overall, most artifacts did yield starch residues, although not always in both Sediments 2 and 3. Phytolith extracts were examined for all HU-7 samples, but for only two Maisabel artifacts due to time constraints: PS2444 (phytoliths present) and PS2451 (unproductive). Phytolith extracts were mounted in Canada balsam. Photomicrographs are presented with supplemental information along with instructions for how to interpret the labeling and matching the photos with the proveniences (Appendix A; Figs. S8–S14).

3.2. *Ecological diversity, richness, evenness, and ubiquity*

To gain new insights into precolonial agricultural economies and ethnobotanical diversity of Puerto Rico, we reviewed the results of all starch studies available for the island utilizing four measures: Shannon diversity index, richness, evenness, and ubiquity. Since phytoliths were studied only for artifacts from Maisabel, HU-7, and one of the other sites reviewed (PO-29), one set of measures was calculated using starch data only. A second set of measures was calculated for Maisabel, HU-7, and PO-29 using starch and phytolith results combined (See Table S3 for the raw data that form the basis for our comparisons.).

Prior to measuring diversity, it is necessary to define the ecological communities under consideration and the collections of organisms that comprise them. In discussing ecological communities, Pielou observed that “one might define as a community the sea birds inhabiting a rocky island …; the arthropods in a rotting log; … the catch of plankton in a single tow of a net; … or the aquatic invertebrates caught in a Surber sampler” (Pielou, 1975: 6). Applying the term “community” to the catches in the plankton net or the Surber sampler “may seem unwarranted since the individual organisms comprising them may not, as a group, have constituted ecological entities before they were caught. Nevertheless, one may wish to know the diversities of such assemblages and they can be classed as communities for convenience” (Pielou, 1975: 6). Hutchinson (1967: 231) introduced the “term *taxocene* for a group of species, all members of a supraspecific taxon and occurring together in the same association” (see also Pielou, 1977: 270).

Pielou’s discussion of organisms captured in sampling devices and Hutchinson’s characterization of a taxocene are relevant for the analysis of starch grains and phytoliths adhering to or embedded in tools collected from archaeological sites. For our purposes, the community is defined as the “catch” of taxa in each set of tools sampled for starches and phytoliths for a defined artifact assemblage. In terms of the taxocene, it is appropriate to include taxa of different taxonomic ranks (i.e., species, genus, family) in measures of ecological diversity. In the current study, diversity and ubiquity values were measured for microbotanical remains identified in given assemblages of artifacts. Assemblages may be defined and ecological diversity indexes calculated at varying spatial and temporal resolutions: artifacts from a site, artifacts from subsections of a given site, or artifacts from a logically grouped set of sites (Farahani and Sinensky, 2022).

It is difficult to impossible to infer all the human behaviors or natural processes that brought individual phytoliths or starch grains onto a tool surface. The assemblage of microfossils captured on/in the surfaces by these complex processes forms a population that can be usefully compared to assemblages from tools of like form, different forms, different contexts, and so on. Differences or similarities among tools may be ascribed to differences or similarities in the behaviors or natural processes that led to microfossil deposition.

Ecologists have devised various measures to characterize diversity within biotic communities (Huston, 1994; Magurran and McGill, 2011; Pielou, 1975, 1977; Stiling, 1999). Common to all biological diversity measures are (1) the number of species or higher taxonomic levels represented in a sample and (2) the proportion of individuals within each identified taxonomic group (Huston, 1994: 65). The number of identified taxa represented in a sample is referred to as ‘richness’ and the equitability of individuals across taxa is called ‘evenness’ (Pielou, 1977: 292, 307–309). Most measures of biological diversity incorporate both properties in statistical formulas (Huston, 1994). One critique of taxonomic diversity indexes is that species abundance could be inversely related to species diversity (Hurlbert, 1971). This critique was “a result of the unreasonable expectation that a single statistic should contain all the information about the assembly of objects that it represents” (Huston, 1994: 66).

One of the most widely used diversity measures is the Shannon index (H'), developed in information statistics (Shannon and Weaver, 1949). The Shannon index is a weighted measure that takes into consideration the relative quantities of the t taxa, thereby necessitating a proportional function p_i ($i = 1, \ldots t$):

$$H' = -\sum_{i=1}^{S}(p_i \ln p_i)$$

where S is the number of taxa in a community, p_i is the proportion of individuals within the ith taxon for a given community, and ln is the natural logarithm (Huston, 1994: 65; Pielou, 1975: 7; Stiling, 1999: 434). As noted by Huston, “it is primarily through comparative studies of the species [or taxonomic] diversity of different communities that an understanding of the mechanisms that regulate diversity can be gained” (Huston, 1994: 68–69).

Evenness (J') is defined as the actual calculated diversity in relation to the maximum possible diversity ($H'_{\max}$) for a given community: $H'_{\max} = \ln Tx$, where Tx is the total number of taxa identified in the community and $J' = H'/H'_{\max} = H'/\ln Tx$. Evenness values range between 0 and 1.0 (Pielou, 1975: 14–17; Stiling, 1999: 434–435). Communities with high levels of equitability (all taxa are relatively equally abundant) will produce similar H' and $H'_{\max}$ indexes.

Richness (number of taxa in a sample) has sometimes been conflated with biological diversity (Huston, 1994: 66–67). Consider for example three hypothetical communities (Table 1). Eleven identified taxa (A–K) are present in Community 1 and Community 2 and four (A–D) in Community 3 (richness). Equitability or evenness in Community 1 is low; in other words, values in column 1 (Abundance) are quite divergent. All taxa are of equal abundance in Community 2 (abundance = 15 for each taxon) and Community 3 (abundance = 4). The identified number of taxa and relative proportions of individuals among the three communities are different resulting in three different diversity indexes:

Community 1 $H' = 0.5755$.
Community 1 $J' = 0.24$.
Community 1 $H'_{\max} = \ln(11) = 2.3979$.
Community 2 $H' = 2.3979$.
Community 2 $J' = 1.0$.
Community 2 $H'_{\max} = \ln(11) = 2.3979$.
Community 3 $H' = 1.3863$.
Community 3 $J' = 1.0$.
Community 3 $H'_{\max} = \ln(4) = 1.3863$.

Communities 2 and 3 with equitable distributions of individuals across taxa result in considerably higher H's than Community 1. In the cases of Communities 2 and 3, $H' = H'_{\max}$. Equitability in Community 1

Table 1
Three hypothetical communities with variable abundance and richness values.

Taxon	Community 1			Community 2			Community 3		
	Abundance	p_i	$p_i \ln p_i$	Abundance	p_i	$p_i \ln p_i$	Abundance	p_i	$p_i \ln p_i$
A	2	0.005348	−0.02797	15	0.090909	−0.21799	4	0.25	−0.34657
B	14	0.037433	−0.12298	15	0.090909	−0.21799	4	0.25	−0.34657
C	1	0.002674	−0.01584	15	0.090909	−0.21799	4	0.25	−0.34657
D	4	0.010695	−0.04853	15	0.090909	−0.21799	4	0.25	−0.34657
E	331	0.885027	−0.10809	15	0.090909	−0.21799			
F	1	0.002674	−0.01584	15	0.090909	−0.21799			
G	6	0.016043	−0.0663	15	0.090909	−0.21799			
H	1	0.002674	−0.01584	15	0.090909	−0.21799			
I	1	0.002674	−0.01584	15	0.090909	−0.21799			
J	4	0.010695	−0.04853	15	0.090909	−0.21799			
K	9	0.024064	−0.08969	15	0.090909	−0.21799			
Total	**374**	**1**	**−0.5755**	**165**	**1**	**−2.3979**	**16**	**1**	**−1.3863**

$H' = -\sum(p_i \ln p_i)$

is low (see especially Taxa E, B, K, and G).

Ubiquity measures the frequency of tools in which a given taxon has been identified in relation to the total number of tools analyzed in an assemblage (Diehl, 2017). Each identified taxon in a defined sample has a ubiquity value expressed as a percentage: Ubiquity = $(ft_i/\mathrm{T})100$, where ft_i is the frequency of tools in which the ith taxon has been identified and T is the total number of tools selected for analysis from a given assemblage. For example, if T = 10 and a given taxon (e.g., *Zea mays*) is found on all 10 tools then the taxon's ubiquity value is 100 percent. Likewise, if the taxon is found on 6 artifacts, then its ubiquity value is 60 percent.

Dating of most of the sites or site components addressed in this paper were based on radiocarbon dates and assessments of chronologically distinctive artifacts. A recent Bayesian analysis of radiocarbon dates from Puerto Rico did not substantially change the calibrated date ranges for the sites included in our study (Rodríguez Ramos et al., 2023). Radiocarbon dates for two sites included in our study were missing from the Bayesian analysis.

4. Results from Maisabel and HU-7

4.1. Maisabel

Except for five human teeth, all of the Early Ceramic Age artifacts studied for phytoliths and starches were griddle fragments (Figs. S1–S3). The Late Ceramic Age artifacts were groundstone or polished stone (Fig. S4). The Maisabel artifacts or teeth preserved identifiable starch grains from maize (*Zea mays*, cf. *Zea mays*), ají (*Capsicum*, cf. *Capsicum*), arrowroot (*Maranta arundinacea*, cf. *Maranta arundinacea*), yuca/manioc (*Manihot esculenta*), squash (*Cucurbita*), cf. *Dracontium* (Araceae), the bean family (Fabaceae), arrowhead (cf. *Saggitaria* sp.), and zamia (cf. *Zamia erosa*) (Tables 2 and 3). In addition, unknown starch granules (unknown starch), hemispheres, altered starch, and "ghost" granules were identified. Simple hemispheres are produced by a number of economic plants and are rarely diagnostic. Altered starch consists of transparent and granular tissues resulting from gelatinization of starch. "Ghost" granules are damaged starch granules that retain a circular outline but lack other features necessary for identification. The designation "cf." in the tables indicates that the starch granule "looks like" the taxon indicated; i.e., cf. *Zea mays* is a granule that looks like maize but cannot be identified beyond a doubt because of damage or obstruction on the slide. Often the problem is that the granule will not rotate to allow the three-dimensional structure to be observed completely. In addition to phytoliths from the palm (Arecaceae) and arrowroot (Marantaceae) families observed in PS2444, a canna phytolith was identified in SS1075 and four artifacts yielded manioc secretory bodies (a very small phytolith type) in starch sediments.

4.2. Site HU-7

Except for one rim sherd of a deep and convex bowl, the HU-7 artifacts studied for phytoliths and starches were griddle fragments (Figs. S5–S7). The artifacts yielded starches from maize (*Zea mays*, cf. *Zea mays*), ají (*Capsicum*, cf. *Capsicum*), yuca/manioc (*Manihot esculenta*), marunguey (cf. *Zamia pumila*), and the bean family (Fabaceae) (Table 4). Altered (gelatinized) starch was also present. Several unknown starch grains were recovered. Phytoliths from canna (cf. *Canna)*, palm family (Arecaceae), and arrowroot family (Marantaceae) were recovered from HU-7 artifacts. Less diagnostic phytoliths included rugulose spheres and a ciliate sphere.

4.3. Discussion of Maisabel and HU-7 results

The tools selected for analysis from Maisabel and HU-7 revealed differential presence or preservation of taxa depending on whether starches or phytoliths were extracted and analyzed. If only starches or only phytoliths are analyzed different suites of plant taxa are represented. Combining the two categories of microremains appears to provide a more accurate or complete representation of the plants that were processed than if only starches or only phytoliths are examined (Table 5).

As measured by ubiquity (percentage presence), there is strong representation of maize *(Zea mays* and cf. *Zea mays* combined) in the assemblages of artifacts from Maisabel (identified on 65% of artifacts) and HU-7 (on all artifacts), most of which are griddle fragments and several groundstone implements from Maisabel (Table S4). Ají (*Capsicum* and cf. *Capsicum* combined) is also well represented at both sites, occurring on 42 percent of Maisabel and 83 percent of HU-7 tools. Manioc is only moderately represented and primarily in the Early Ceramic Age artifacts from Maisabel (23%). Arrowroot (*Maranta arundinacea*) and the remaining taxa are present in trace amounts in the Maisabel assemblage. The representation of root/tuber plants on HU-7 artifacts is similar. Interestingly, this pattern of greater representation (ubiquity) and more abundant microremains of maize than manioc and other root/tuber plants is often the case for artifacts from the Neotropics (Table S4) (e.g., Berman and Pearsall, 2020; Pearsall et al., 2020; but see Pagán-Jiménez and Oliver, 2008).

Maize and ají co-occurred in 75 percent and 83 percent of the Maisabel Mounded Midden 2 and HU-7 artifacts, respectively. By contrast, even though maize and ají also dominated the Mounded Midden 1 assemblage they only co-occurred in 17 percent of those artifacts. A rim sherd of a deep and convex bowl from HU-7 produced one cf. *Capsicum* starch grain.

Arrowroot starch is encountered relatively rarely even when arrowroot family phytoliths are present. This is more than likely a

Table 2
Results of the Maisabel Early Ceramic Age starch grain and phytolith analyses.

Context	Catalog Number	Artifact Description	PS#	SS#	Sediment	No Starch	No Economic Phytoliths	Taxon (starch)	Taxon (phytoliths)	Other
Mounded Midden 1	1.119.27	Griddle sherd	1879	90	2	X				oil (P)
			1880	91	3			1 *Zea mays*, 1 cf. *Z. mays*		1 unknown starch, 3 altered starch, 2 “ghost” granules
		Griddle sherd	1881	92	2			1 cf. *Capsicum*		1 “ghost” granule
			1882	93	3			2 *Capsicum*; 1 *Maranta arundinaceae*, arrowroot	3 *Manihot esculenta* secretory bodies	7 altered starch
		Griddle sherd	1878	89	3				1 *Manihot esculenta* secretory body	5 altered starch, 1 “ghost” granule
		Griddle sherd	1883	94	2			2 *Zea mays*		
			1884	95	3				3 *Manihot esculenta* secretory bodies	7 altered starch, 5 “ghost” granules
		Griddle sherd	1836	74	1			3 *Zea mays*		1 “ghost” granule
			1839	77	2			3 *Zea mays*, 1 cf. *Capsicum*, 1 *Maranta arundinaceae*, 1 cf. *Maranta arundinaceae*, 1 cf. *Dracontium*		1 starch hemisphere, 2 “ghost” granules, 1 oil
			1840	78	3	X				
	1.34.16	Griddle sherd	2442	421	2			6 *Zea mays*		1 unknown starch
			2443	422	3	X				1 cellulose ring
	1.35.12	Griddle sherd	2444	423	2	X			Rugulose spheres (P), 1 Arecaceae palm family sphere, 1 Marantaceae nodular	
			2445	424	3	X				
	1.36.22	Griddle sherd	2446	425	2			2 *Zea mays*		
			2447	426	3	X				
	1.37.13	Griddle sherd	2448	427	2			1 *Capsicum*		
			2449	428	3	X				
	1.38.7	Griddle sherd	2450	429	2			2 *Zea mays*, 1 cf. *Zea mays*, 1 cf. *Capsicum*		
			2451	430	3	X	X			
	1.40.13	Griddle sherd	3495	1073	2					1 unknown starch
			3496	1074	3			1 *Zea mays*		1 altered starch
	1.41.16	Griddle sherd	3497	1075	2			2 *Capsicum*	1 cf. *Canna* sphere	1 altered starch
			3498	1076	3					1 altered starch, 1 “ghost” granule
	1.43.11	Griddle sherd	3499	1077	2			1 *Capsicum*		1 altered starch
			3500	1078	3					1 altered starch
	1.44.16	Griddle sherd	3501	1079	2					altered starch (P)
			3502	1080	3					altered starch (P)
	1.45.13	Griddle sherd	3503	1081	2					altered starch (P), blackened tissue (P)
			3504	1082	3			1 *Capsicum*		2 “ghost” granules, blackened tissue (P), 2 cf. faceted spores
	1.46.12	Griddle sherd	3505	1083	2	X				
			3506	1084	3			2 *Zea mays*		altered starch (P), “ghost’ granule (P)
	1.47.11	Griddle sherd	3507	1085	2			1 *Zea mays*		altered starch (P), blackened tissue (P)
			3508	1086	3					altered starch (P), 1 “ghost’ granule, blackened tissue (P), 1 perforated tissue
	1.48.6	Griddle sherd	3509	1087	2			2 *Zea mays*, 3 *Capsicum*, 1 Fabaceae		1 unknown starch, altered starch (P), 1 epidermal tissue, 1 cf. faceted spore

(*continued on next page*)

Table 2 (*continued*)

Context	Catalog Number	Artifact Description	PS#	SS#	Sediment	No Starch	No Economic Phytoliths	Taxon (starch)	Taxon (phytoliths)	Other
			3510	1088	3			1 *Zea mays*		
Maisabel Burial 5[a]		Tooth						7 cf. *Sagittaria* sp., 2 cf. *Zamia erosa*, 1 *Zea mays*		4 unknown starch
Maisabel Burial 14[b]		Tooth						1 *Zea mays*		1 unidentified starch
Maisabel Burial 17[c]		Tooth						1 cf. *Zea mays*, 1 cf. *Manihot esculenta*		1 unidentified starch
Maisabel Burial 21[d]		Tooth						1 *Manihot esculenta*, 1 cf. *Manihot esculenta*		2 clusters unidentified starches

[a] Burial excavated and described by Siegel (1992: 207, Fig. 5.9) and starch residues identified by Mickleburgh and Pagán-Jiménez (2012: Table 2).
[b] Burial excavated and described by Siegel (1992: 226–228, Fig. 5.19) and starch residues identified by Pagán-Jiménez and Mickleburgh (2023: Table S2).
[c] Burial excavated and described by Siegel (1992: 211–213, Fig. 5.12) and starch residues identified by Pagán-Jiménez and Mickleburgh (2023: Table S2).
[d] Burial excavated and described by Siegel (1992: 215, Fig. 5.14) and starch residues identified by Pagán-Jiménez and Mickleburgh (2023: Table S2).

Table 3
Results of the Maisabel Late Ceramic Age starch grain and phytolith analyses.

Context	Catalog Number	Artifact Description	PS#	SS#	Sediment	No Starch	No Economic Phytoliths	Taxon (starch)	Taxon (phytoliths)	Other
Mounded Midden 2	1.23.21	Groundstone fragment	1819	57	2			1 *Cucurbita*		1 starch hemisphere
			1820	58	3			2 *Zea mays*, maize; 1 cf. *Capsicum*, aji; 1 *Fabaceae*, bean		
	1.18.141	Groundstone fragment	1837	75	2	X				
			1838	76	3			1 *Zea mays*		
	1.19.35	Metate-like polished stone	1885	96	2	X				raphid oil (P)
			1886	97	3			4 *Zea mays*, 4 *Capsicum*	1 *Manihot esculenta*, yuca, secretory body	1 unknown starch
	1.789.49	Groundstone tool	1887	98	2	X				oil (P)
			1888	99	3			7 *Zea mays*, 1 cf. *Zea mays*, 2 cf. *Capsicum*, 1 Fabaceae		1 unknown starch

Table 4
Results of the HU-7 starch grain and phytolith analyses.

Context	Catalog Number	Artifact Description	PS#	SS#	Sediment	No Starch	No Economic Phytoliths	Taxon (starch)	Taxon (phytoliths)	Other
Buried midden deposits	Bag 1099 (S-1)	Rim sherd of a deep and convex bowl	2410	405	2		X	1 cf. *Capsicum*		
			2411	406	3		X	1 *Zea mays*		1 altered starch
	Bag 1099 (S-2)	Griddle sherd	2412	407	2		X	10 *Zea mays*, 2 cf. *Zea mays*, 1 *Manihot esculenta*		
			2413	408	3		X	1 *Zea mays*, 2 *Capsicum*		1 cellulose ring
	Bag 1090 (S-3)	Griddle sherd	2414	409	2			1 *Zea mays,* 1 cf. *Zamia pumila*	1 Marantaceae nodular	1 unknown starch
			2415	410	3			5 *Zea mays*, 1 Fabaceae	1 Marantaceae conical	1 raphid
	Bag 1080 (S-4)	Griddle sherd	2416	411	2	X			9 Arecaceae spheres, 10 Marantaceae nodular	6 rugulose spheres, 1 ciliate sphere
			2417	412	3		X	1 *Zea mays*, 1 *Capsicum*		1 ghost granule
	Bag 187 (S-5)	Griddle sherd	2418	413	2			2 *Zea mays*, 1 cf. *Zea mays*, 1 *Capsicum*	1 cf. *Canna* sphere, 4 Marantaceae nodulars	1 rugulose sphere
			2419	414	3	X	X			
	Bag 215 (S-6)	Griddle sherd	2420	415	2			1 *Capsicum*	1 Marantaceae nodular	3 altered starch
			2421	416	3		X	3 *Zea mays*		2 altered starch

Table 5
Summarized taxa identified in Maisabel and HU-7 by tool types.

Site/Context	Tool Type	Taxa Ordered by Frequency (high to low)
Maisabel Mounded Midden 1	18 griddle sherds (3.2 grains/artifact)	57 starch/phytolith grains: 29 *Zea mays* 13 *Capsicum* 7 *Manihot esculenta* 3 *Maranta arundinaceae* 1 *Dracontium* 1 Arecaceae 1 Marantaceae 1 *Canna* 1 Fabaceae
Maisabel Burial 5	1 tooth (10 grains/tooth)	10 starch/phytolith grains: 7 *Sagittaria* sp. 2 *Zamia amblyphyllidia* 1 *Zea mays*
Maisabel Burial 14	1 tooth (1 grain/tooth)	1 *Zea mays*
Maisabel Burial 17	1 tooth (2 grains/tooth)	1 cf. *M. esculenta* 1 cf. *Zea mays*
Maisabel Burial 21	1 tooth (2 grains/tooth)	1 *M. esculenta* 1 cf. *M. esculenta*
Maisabel Mounded Midden 2	4 ground/polished stone artifacts (6.5 grains/artifact)	26 starch/phytolith grains: 15 *Zea mays* 7 *Capsicum* 2 *Fabaceae* 1 *Cucurbita* 1 *Manihot esculenta*
HU-7	6 griddle sherds (10.5 grains/artifact)	63 starch/phytolith grains: 27 *Zea mays* 17 Marantaceae 9 Arecaceae 6 *Capsicum* 1 *Manihot esculenta* 1 *Zamia pumila* 1 Fabaceae 1 *Canna* sphere

preservation issue—the starch granules are large and very distinctive, but also fragile and easily torn. They can disappear after slide-scanning and exposure to heat from the instrument light. Three Mounded Midden 1 and four HU-7 griddle fragments produced arrowroot or arrowroot family microfossils (3 starch, 18 phytoliths). Except for one, all the manioc grains were phytoliths suggesting that manioc may be underrepresented in studies focusing exclusively on starches. Reasons for this are obscure. Starch grains are abundant in manioc comparative samples, and do not appear to be any more fragile than maize (Pearsall's observation). Presence of gelatinized starch tissues indicates application of heat, i.e., cooking or processing of cooked foods. While some of the patterning described here may be a product of taphonomic or preservational factors, we believe the relative importance of maize, ají, manioc, and arrowroot on Maisabel and HU-7 artifacts is consistent with a growing number of microbotanical studies in the Caribbean (Pagán-Jiménez, 2013).

Rouse (1948: 523) stated long ago that the Taínos collected wild arrowroot to use in the pepper pot. Sturtevant (1961: 71, 76; 1969: 184–189) claimed that arrowroot was introduced to the Greater Antilles in the seventeenth century from Barbados and was not used aboriginally in the West Indies. Our finding of arrowroot grains in both Early and Late Ceramic Age contexts indicates its long use in precolonial Puerto Rico (see also Pagán-Jiménez, 2022; Pagán-Jiménez and Oliver, 2008: 152–153) and it has been documented in c. 7000BP contexts elsewhere in the New World tropics (Piperno et al., 2000).

The importance of maize in the West Indian precolonial diet has long been debated. Based on ethnohistoric sources, Sturtevant (1961: 70–71) argued that it was a secondary food item to manioc or sweet potatoes. Newsom suggested that maize was a late prehistoric introduction to the Caribbean from northeastern South America and was restricted to the elite stratum of Taíno chiefly society (Newsom and Wing, 2004: 202–203, 214). As discussed earlier, environmental coring along one edge of the Maisabel site produced maize phytoliths in a context dating to the Archaic (Fig. 3). Maize was by far the dominant taxon in the Maisabel mounds and HU-7 deposit, represented exclusively by starch grains (Table 6). At this stage of research, maize appears to have played an important role throughout the Caribbean Ceramic Age and there is growing evidence for its use during the Archaic as well (Chinique de Armas et al., 2015; Pagán-Jiménez, 2013).

In contrast to conventional thinking and in agreement with other microbotanical studies, manioc was used less intensively at Maisabel and HU-7 than other plants, especially maize, ají, and arrowroot/arrowroot family (Table 6). Interestingly, 78 percent of the artifacts with manioc microfossils came from Maisabel Mounded Midden 1 (N90W13, 60–70 cm), an Early Ceramic Age context (Table 2: Catalog Number 1.119.27). These artifacts were collected from a context underlying a charcoal sample that dated to cal AD80–410 (Table S1: N90W13, 40–50 cm). Although the microfossil sample size was small (n = 9), this finding suggests that manioc may have been more consistently used by the earliest Ceramic Age colonists to the West Indies from lowland South America than either before or after that time. Eight of the manioc grains were phytoliths (all Maisabel), and one was starch (HU-7). The concentration of manioc grains with Early Ceramic Age artifacts in Maisabel may be a sampling issue since Pagán-Jiménez identified manioc starch in several Late Ceramic Age sites (CE-11, Cueva de los Muertos, Vega de Nelo Vargas) (Table S3).

There is agreement across ethnohistoric accounts in the Greater Antilles that a variety of root and seed crops was cultivated (Benzoni, 2017; Colón, 1959; Las Casas, 1951; Oviedo, 1959). Regarding maize, Oviedo (1959: Chapter 4) noted that "On the islands the grain is roasted. Also, when the ears are tender they are eaten almost like milk." Colón (1959: Chapter 28) documented three methods of maize processing: "a grain resembling panic grass that they call maize and is most tasty, boiled, roasted, or ground into flour." Benzoni described preparation of corn meal that he observed in early sixteenth-century Hispaniola:

> They take a bit of this grain and wet it thoroughly with some cold water in the evening. In the morning they slowly break it into pieces with two stones … They make the dough with wet hands and shape them into little breads, some long, some round. Then they cook them. This is the bread of the commoners. [Benzoni, 2017: 43]

Our findings of numerous maize starch grains on groundstone tools and griddles confirm at least the floured form of corn described by Colón (see also Sauer, 1966: 54–55). The co-occurrence of maize and ají grains

Table 6
Frequencies and percentages of Early versus Late Ceramic Age plant taxa identified in the Maisabel and HU-7 artifacts[a].

Taxon/Total Grains Identified	Early Ceramic Age (22 artifacts [69% of total])	Late Ceramic Age (10 artifacts [31% of total])
Z. mays/73	N = 31 (42.5%), E = 50	N = 42 (57.5%), E = 23
Capsicum/26	N = 13 (50%), E = 18	N = 13 (50%), E = 8
M. esculenta/15	N = 10 (83.3%), E = 10	N = 2 (16.7%), E = 5
M. arundinaceae/3	N = 3 (100%), E = 2	N = 0 (0%), E = 1
Marantaceae/18	N = 1 (5.6%), E = 12	N = 17 (94.4%), E = 6
Dracontium/1	N = 1 (100%)	N = 0 (0%)
Arecaceae/10	N = 1 (10%), E = 7	N = 9 (90%), E = 3
Canna/2	N = 1 (50%), E = 1	N = 1 (50%), E = 1
Fabaceae/4	N = 1 (25%), E = 3	N = 3 (75%), E = 1
Cucurbita/1	N = 0 (0%)	N = 1 (100%)
Z. pumila/1	N = 0 (0%)	N = 1 (100%)
Z. amblyphyllidia/2	N = 2 (100%), E = 1	N = 0 (0%), E = 1
Sagittaria sp./7	N = 7 (100%), E = 5	N = 0 (0%), E = 2

[a] N represents the frequency and percentage of starch grains and phytoliths identified for a given taxon. E represents the expected frequency of starch grains and phytoliths for a given taxon based on the relative numbers of analyzed artifacts and assuming consistent use of the taxon during the Early and Late Ceramic Ages. Example: E for Early Ceramic Age maize grains = (73 total grains x 22 artifacts)/32 total artifacts = 50.

on many of the artifacts, especially griddles, suggests that these two domesticates may have been combined to make a spicy cornbread or alternatively the two plants were processed at different times for different purposes using the same artifacts.

The Maisabel and HU-7 microbotanical findings will now be compared to other similar studies available for Puerto Rico. In addition to comparing the kinds of taxa represented geographically and through time, ecological measures of diversity, richness, and evenness will be examined.

5. Ethnobotanical diversity in precolonial starch and phytolith assemblages from Puerto Rico

The Maisabel and HU-7 findings add to the growing database of microbotanical evidence for a broad range of cultigens nurtured through the Ceramic Age of Puerto Rico. While these findings are generally consistent with ethnohistoric accounts, we agree with DeBoer's (1975) caution about assuming primacy of bitter manioc as the staple crop of choice based on great quantities of ceramic griddles and microflakes in Ceramic Age deposits. Numerous other studies discussed earlier have demonstrated that his cautionary note was well founded. It is becoming increasingly clear that maize played an important role in subsistence through the c. 2000-year Ceramic Age. Maize starch grains dominated the Early and Late Ceramic Age assemblages from Maisabel and HU-7. *Capsicum* was also a favored cultigen in both sites, especially Maisabel. Maize and *Capsicum* frequently co-occurred in the same artifacts suggesting that they may have been processed together. Alternatively, the same artifacts may simply have been used to process a variety of plants at different times resulting in palimpsest assemblages of residues.

Artifact collections from a number of sites spanning the Archaic and Ceramic Ages in Puerto Rico have now been sampled for microbotanical analyses (Table 7). To compare results of these studies ecological measures of diversity, richness, and evenness were applied to the starch and phytolith data (Table 8). In the case of multicomponent sites, assemblages were divided and analyzed by the distinct components or occupations as identified by the excavators. Table 8 is organized in order from lowest to highest diversity values (H'). Evenness values (J') imperfectly followed the same progression. Maximum possible diversities ($H'_{\max}$) were determined by equitability and richness (see earlier discussion regarding hypothetical communities). As we will show, diversity (H') and evenness (J') values generally relate to site sizes or occupational intensity and perhaps relative degrees of specialization in activities within a given settlement. Sites with the greatest H' values are associated with intensively occupied settlements during the Archaic and Early Ceramic Ages.

Maruca is an Archaic site occupied from c. 3000–500BC (Rodríguez 1999). It had among the highest ethnobotanical diversity and evenness values in our study population. The findings from Rodríguez's (1999) excavations required Caribbean archaeologists to revise their thinking about Archaic lifeways and adaptations. In contrast to a small, short-term occupation of hunters-gatherers-foragers-collectors, Maruca represented a permanent, intensively occupied settlement with structural remains (postmolds), human burials, midden deposits, and workshops and activity areas (Rodríguez, 1999). Recent findings from the Ortiz site in southwestern Puerto Rico also support a picture of sedentary groups, and perhaps even territorial settlement organization, in the Archaic (Pestle et al., 2023).

Based on his starch residue analysis of four artifacts from Maruca as well as artifacts from other Archaic sites, Pagán-Jiménez (2009; Pagán-Jiménez et al., 2005) is further requiring us to rethink Archaic subsistence strategies. Starch grains from maize, cf. manioc, yautías, and batatas were identified, cultivars normally associated with Ceramic Age sites. Pagán-Jiménez also examined artifacts from a Late Archaic context in Puerto Ferro, a small burial site in Vieques (Chanlatte Baik and Narganes Storde, 1991). Diversity and evenness values there were low, although notably maize and possibly manioc and batatas were identified (Pagán-Jiménez, 2009; Pagán-Jiménez et al., 2005).

Aside from Maruca, other assemblages producing higher ethnobotanical diversity and evenness scores came from Early Ceramic Age contexts (Huecoid/Saladoid). The Maisabel (Early Ceramic Age context), King's Helmet, La Hueca, and Punta Candelero sites had the highest H' and J' values. These sites were intensively occupied with activities ranging from domestic to ritual and numerous artifact classes were present. As Early Ceramic Age colonizers coming out of northeastern South America and quickly settling the Lesser Antilles up through eastern Hispaniola, the high H' values are consistent with the highly diverse tropical forest agricultural system of greater Amazonia. We would expect to see measures of high plant diversity, regardless of whether the sites themselves were large or small. Coevolutionary theory suggests that over time agriculture tends to become focused more intensively on fewer, productive crops (Pearsall, 2009). As Newsom and Pearsall have discussed, the Caribbean crop mix also represents unique adaptations to Caribbean environments (Newsom and Pearsall, 2003; Newsom and Wing, 2004).

The Late Ceramic Age assemblages generally have lower ethnobotanical diversity and evenness values (lowest diversity [$H' <$ about 1] and evenness [$J' <$ about 0.6]). The Maisabel results are illustrative of the difference between the Early and Late Ceramic Age pattern. Artifacts from Mounded Midden 1 and teeth from Burials 5, 14, 17, and 21 (Saladoid, Early Ceramic Age) produced amongst the highest diversity and evenness scores (starch and phytoliths combined). Mounded Midden 2 (Ostionoid, Late Ceramic Age) artifacts produced considerably lower values for diversity and evenness. The very small Late Archaic Puerto Ferro site also produced low ethnobotanical diversity and

Table 7
Sites from precolonial Puerto Rico studied for phytoliths and/or starch grains.

Site	Description	Reference
AR-39	Late Saladoid/Early Ostionoid habitation (c. AD350–770).	Pagán-Jiménez (2008)
CE-11	Hilltop habitation. Santa Elena/ Esperanza occupations (c. AD1000–1270).	Pagán-Jiménez (2011b); Pagán-Jiménez and Carlson (2014)
CE-33	Hillside terrace habitation site. Esperanza occupation (c. AD1410–1470).	Pagán-Jiménez (2011b)
Cueva de los Muertos	Cave burial site of ritual significance. Ostiones occupation (c. AD700–1200).	Pagán-Jiménez and Oliver (2008)
HU-7	Small short-term village occupied during the transition between the Monserrate and Santa Elena periods (c. AD900/1000).	This study
King's Helmet	Late Saladoid habitation (c. AD650–800).	Pagán-Jiménez (2011c)
La Hueca	Huecoid/Saladoid intensively occupied settlement (c. 200BC–AD1000)	Pagán-Jiménez (2007)
Maisabel	Large intensively occupied settlement (c. 340BC–AD1200).	This study; Mickleburgh and Pagán-Jiménez (2012); Pagán-Jiménez and Mickleburgh (2023)
Maruca	Archaic domestic site (c. 2890–395BC).	Pagán-Jiménez et al. (2005)
PO-29	Large civic-ceremonial-habitation site with two major occupations: Cuevas/Monserrate (c. AD650–900) and Esperanza (c. AD1300–1500).	Espenshade et al. (2014)
Punta Candelero	Late Saladoid domestic site (c. AD600–860).	Pagán-Jiménez (2007)
Puerto Ferro	Multiple short-term occupations during the Archaic (c. 2140–700BC).	Pagán-Jiménez et al. (2005)
Vega de Nelo Vargas	Residential farmstead with domestic and ritual activities (c. AD1280–1430).	Pagán-Jiménez and Oliver (2008)

Table 8

Diversity and evenness values calculated for taxa identified in starch and phytolith assemblages from Puerto Rico ordered from lowest to highest diversity.

Archaeological Site	Shannon Diversity Index (H')	Maximum Possible Diversity ($H'_{\max}$)	Evenness (J')	Data Source
PO-29 (starch only) (N = 16)	0	0	N/A	Espenshade et al. (2014)
Vega de Nelo Vargas (N = 3) Residential farmstead with domestic and ritual activities (*batey*) (c. AD1280–1430).	.575	2.398	.24	Pagán-Jiménez and Oliver (2008)
HU-7 (starch only) (N = 6) Small short-term village occupied during the transition between the Monserrate and Santa Elena periods (c. AD900/1000).	.706	1.386	.509	This study
Cueva de los Muertos (N = 3) Cave burial site of ritual significance. Ostiones occupation (c. AD700–1200).	.795	2.708	.294	Pagán-Jiménez and Oliver (2008)
Puerto Ferro (N = 2) Small Archaic burial site.	.811	1.946	.417	Pagán-Jiménez (2009); Pagán-Jiménez et al. (2005)
CE-33 (N = 3) Hillside terrace habitation site. Esperanza occupation (c. AD1410–1470).	.957	1.792	.534	Pagán-Jiménez (2011a)
Maisabel Mounded Midden 2 (starch only) (N = 4) Large intensively occupied settlement; Late Ceramic Age occupation.	.994	1.386	.717	This study
PO-29 (starch and phytoliths) (N = 16) Large civic-ceremonial-habitation site with two major occupations: Cuevas/Monserrate (c. AD650–900) and Esperanza (c. AD1300–1500).	1.044	1.792	.582	Espenshade et al. (2014)
CE-11 (N = 5) Hilltop habitation. Santa Elena/Esperanza occupations (c. AD1100–1270).	1.082	2.197	.493	Pagán-Jiménez (2011a)
Punta Candelero La Hueca Phase 2 (N = 8) Late Saladoid domestic site (c. AD600–860).	1.086	2.398	.453	Pagán-Jiménez (2007)
Maisabel Mounded Midden 2 (starch and phytoliths) (N = 4) Large intensively occupied settlement; Late Ceramic Age occupation.	1.119	1.609	.695	This study
Maisabel Mounded Midden 1 and Burials 5, 14, 17, 21 (starch only) (N = 22) Large intensively occupied settlement; Early Ceramic Age occupation (c. 340BC–AD700).	1.493	2.079	.718	This study; Mickleburgh and Pagán-Jiménez (2012); Pagán-Jiménez and Mickleburgh (2023)
HU-7 (starch and phytoliths) (N = 6) Small short-term village occupied during the transition between the Monserrate and Santa Elena periods (c. AD900/1000).	1.482	2.079	.712	This study
King's Helmet (N = 5) Late Saladoid habitation (c. AD650–800).	1.483	1.792	.828	Pagán-Jiménez (2011b)
Punta Candelero La Hueca Phase 1 (N = 5) Late Saladoid domestic site (c. AD600–860).	1.558	2.398	.649	Pagán-Jiménez (2007)
AR-39 (N = 6) Late Saladoid/Early Ostionoid habitation (c. AD350–770).	1.602	1.792	.894	Pagán-Jiménez (2008)
Maisabel Mounded Midden 1 and Burials 5, 14, 17, 21 (starch and phytoliths) (N = 22) Large intensively occupied settlement; Early Ceramic Age (c. 340BC–AD700).	1.699	2.398	.708	This study; Mickleburgh and Pagán-Jiménez (2012); Pagán-Jiménez and Mickleburgh (2023)
Punta Candelero (N = 14) Late Saladoid domestic site (c. AD600–860). Cuevas component	1.712	2.197	.779	Pagán-Jiménez (2007)
Maruca (N = 4) Archaic domestic site (c. 2890–395BC).	1.826	2.079	.878	Pagán-Jiménez (2009); Pagán-Jiménez et al. (2005)
La Hueca Phase 2 (N = 15) Large intensively occupied settlement; Early Ceramic Age	1.966	2.398	.819	Pagán-Jiménez (2007)
La Hueca Phase 3 (N = 9) Large intensively occupied settlement; Early Ceramic Age	1.980	2.197	.901	Pagán-Jiménez (2007)
La Hueca Phase 1 (N = 9) Large intensively occupied settlement; Early Ceramic Age	2.039	2.565	.795	Pagán-Jiménez (2007)

evenness values.

Site HU-7 exemplifies the problem with analyzing starch grains exclusively. Based on starch grains only, HU-7 ranked nearly the lowest in diversity (H' and $H'_{\max}$) and evenness. When phytoliths are included, diversity and evenness scores are considerably higher, placing the site as transitional between low and high in the diversity distribution. HU-7 was a small, relatively short-term village occupied during the Monserrate-Santa Elena period, which Roe (1989: 292) suggested was a time of transition between the Early (Saladoid) and Late (Ostionoid) Ceramic Ages in Puerto Rico.

Vega de Nelo Vargas was a small household-based settlement with a civic-ceremonial plaza (*batey*) occupied in late prehistory/protohistory, c. AD1280–1430 (Pagán-Jiménez and Oliver, 2008). It may have been a small tributary center within the political sphere of the large, monumental center of Caguana less than 2 km away. Cueva de los Muertos is a cave with petroglyphs and four human burials and is also located within 2 km of Caguana. The site dates to c. AD700–1100 and overlaps with the earliest occupation of Caguana (Pagán-Jiménez and Oliver, 2008). Vega de Nelo Vargas and Cueva de los Muertos are small sites and the low H' diversity indexes likely reflect the specialized uses of the places. Note the very high $H'_{\max}$ values of both sites indicating relatively large ranges of taxa represented with a few dominant taxa (low equitability or evenness).

6. Discussion

6.1. Impact of sample size on results

The diversity trends identified here suggest significant changes over time in subsistence strategies. It is important to consider to what extent these trends are artifacts of sampling. We were concerned whether there was a correlation between numbers of artifacts per site or context analyzed and diversity and evenness measures. Graphing diversity and evenness versus sample size produced point scatters with low positive trendlines and r product moment correlation coefficients of 0.458 and 0.327 for diversity and evenness, respectively (Fig. 5). There are four datasets with greater than 10 artifacts, three of which are highly diverse resulting in a slightly elevated trendline. For the 14 datasets with less than 10 artifacts, there is no discernible trend between sample size and diversity or evenness. Given these low correlations between sample size and diversity/evenness, we feel confident, therefore, that our results are not impacted by numbers of artifacts studied beyond a negligible degree of inflation in the largest datasets relative to the others (Hinkle et al., 2003: Table 1).

6.2. Patterns of ethnobotanical diversity in precolonial Puerto Rico

What is clear, the earliest Archaic occupations documented for Puerto Rico incorporated the cultivation of domesticated plants into their resource base, including maize, batatas, and manioc. This was a subsistence system of high ethnobotanical diversity. The earliest occupants of the Greater Antilles most likely came from Central America (Wilson et al., 1998). Evidence for the use of a variety of plants has been documented in Central America dating to c. 5000 years ago and earlier. These include arrowroot, manioc, batatas, squash, maize, chiles, cotton, palms, nance, hoplum, and sapotes (Piperno and Pearsall, 1998: 286–310). Cultigens identified in Archaic contexts from the Greater Antilles likely were introduced with the earliest colonizers from Central America (Chinique de Armas et al., 2015).

The Saladoid colonizers into the islands also brought their lifeways and adaptive strategies, including a suite of cultigens, from Amazonia (Keegan and Hofman, 2017; Lathrap, 1970; Rouse, 1992; Siegel, 1989, 1991a; Wilson, 2007). Once Archaic and Ceramic Age people independently dispersed into the islands from Central and South America by c. 4500/6000BC and 500/700BC, respectively, there would have been ongoing relations and transport of items, including plants, between the colonized and homeland areas (Hofman et al., 2007; Keegan and Hofman, 2017).

Based on pollen, residue, macrobotanical, and land-use history studies the picture emerging is one of Archaic agricultural practices originating in Central America, eventually combining with Early Ceramic Age practices derived from greater Amazonia. There is a strong negative trend over time in the diversity values of the Ceramic Age datasets examined in this study, a pattern consistent with expectations from human behavioral ecology discussed below ($r = -0.821$) (Fig. 6).

By the Late Ceramic Age, a subsistence system of markedly lower ethnobotanical diversity was present in Puerto Rico. This system supported growing populations and increased social and political complexity (Curet, 2005: 226–228; Siegel, 2004). There is archaeological and ethnohistoric evidence for feuding and warfare between increasingly competitive chiefly polities in Puerto Rico, especially by c. AD1300 (Siegel, 2004, 2011). Low agricultural diversity could be a risky strategy in the context of heightened competition and conflict. In historical settings of population growth resulting eventually in territorial pressure, resource imbalances, or both, some form of "remedial action" is necessary (Ferguson, 1990: 32). The primary options documented ethnographically include intensification of production, greater emphasis on external trade relations, out-migration, and/or heightened levels of warfare (Balée, 1988; Carneiro, 1981, 1990; Ferguson, 1990; Kirch, 1984, 1990; Netting, 1974). One risk-minimizing strategy in this context of low agricultural diversity and heightened interpolity feuding is to store large quantities of staple items to feed the polity and luxury items to maintain the ideology. Evidence of both practices is documented in ethnohistoric accounts (Colón, 1959; Dunn and Kelley, 1989; Las Casas, 1951; Sauer, 1966). In synthesizing the ethnohistoric accounts, Moscoso reported that tributary relations characterizing protohistoric chiefly polities in the Greater Antilles resulted in storable surpluses, including "specialized handicrafts … innumerable ritual objects … ceremonial garb, and … agricultural and marine foodstuffs" (Moscoso, 1981: 270).

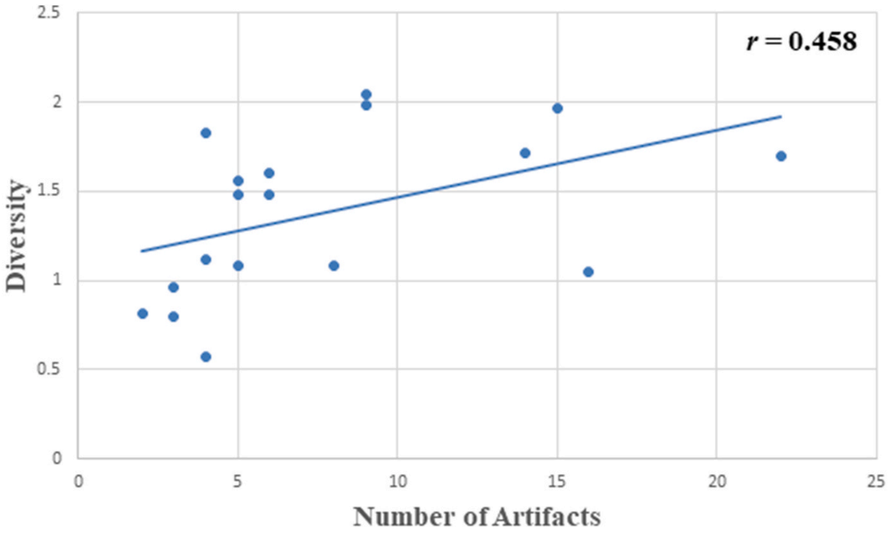
Distinctive species or varieties of cultigens may have been introduced separately by Archaic and earliest Ceramic Age settlers of the West Indies. While identifying the precise timing of plant introductions may be challenging, recovery and analysis of macroremains and microfossils from well-dated contexts may help to clarify the process and implications of these contributions by different groups of people (Newsom and Pearsall, 2003; Newsom and Wing, 2004).

Microbotanical studies of residues from Caribbean artifacts are complementing the more traditional macrobotanical studies that have been undertaken for decades. Examining residues adhering to or embedded in the tools used for preparing foods provides a somewhat more intimate or direct glimpse into subsistence strategies than macroremains found in midden deposits. Residue studies provide direct behavioral links between food remains (starches, phytoliths) and their archaeological contexts. In the case of artifacts, the direct links are the tools used for processing/serving/consuming foodstuffs. For dentition, it is a direct link to consumption of a foodstuff by an individual. Direct behavioral linkages allow for more nuanced interpretations of subsistence practices. For charred macroremains, the behavior that produced them was burning and links to other behaviors like consumption is indirect. We are not advocating for the superiority of micro over macroremains analysis; they are complementary. Going forward, we suggest that both starch grains and phytoliths systematically be incorporated into microbotanical analyses, providing a more accurate reconstruction of plant use than if only one or the other line of evidence is followed.

6.3. Agricultural evolution in Puerto Rico (and the Caribbean)

The evidence emerging from studies across the Caribbean shows that plant domesticates were brought to many of the islands by the earliest and later colonists. Maize, manioc, batatas, beans, arrowroot, and perhaps other domesticates appear to have been introduced by Archaic colonists from Central America to the Greater Antilles by possibly c. 4500BC (Newsom and Wing, 2004). A similar suite of domesticates was introduced to Trinidad by nearly 6000BC (Pagán-Jiménez et al., 2015). Dispersal into the Lesser Antilles and Puerto Rico by Saladoid colonists beginning c. 500/700BC brought yet another set of domesticates from Greater Amazonia (Lathrap, 1970; Newsom and Wing, 2004; Siegel, 1989) (Fig. 7).

The earliest stages of agricultural evolution, including incidental domestication that characterized low-level food production took place in mainland areas of Central and South America prior to entry of people into the islands (Pearsall, 1995, 2009; Piperno and Pearsall, 1998; Rindos, 1984; Smith, 2001). As people entered the islands bringing a subset of their homeland cultivars with them, landscapes needed to be modified accordingly in order to create patches of sufficient sizes to cultivate and propagate their transported plant domesticates. We now have paleoenvironmental records including profiles of charcoal particulates that document anthropogenic landscapes and forest clearing dating to the full range of human occupations in many of the islands (Burney et al., 1994; Siegel, 2018; Siegel et al., 2005, 2015). The picture emerging from paleoenvironmental and ethnobotanical studies suggests that coevolutionary processes of landscape modification/management, incidental domestication or protocultivation,



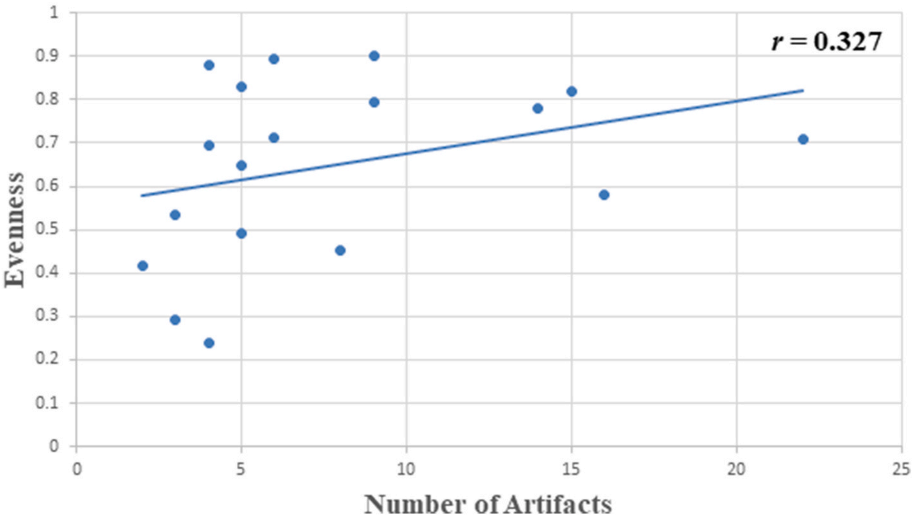


Fig. 5. Diversity and evenness plotted against the number of artifacts analyzed per site or site context. Both plots produced low positive trendlines and *r* product moment correlation coefficients: diversity = 0.458 and evenness = 0.327. Three of the datasets with greater than 10 artifacts caused the trendlines to be slightly elevated.

and plant selection/manipulation/domestication/dispersal had occurred in mainland areas prior to colonizing the islands. Once in the islands, people quickly established swidden or garden plots following strategies that had been developed in their homeland regions.

As people colonize new areas, there is a process of landscape and resource learning, whereby the usefulness of local wild biota is recognized and exploited along with transported domesticates (Rockman and Steele, 2003). Especially for colonizers bringing a subset of their homeland domesticates to new places, it is expected that biotic resources will be evenly exploited over a relatively wide range of taxa; in these cases, species diversity in ethnobotanical assemblages should be high. “Unless one grants … early farmers a phenomenal amount of good luck and even better judgement, it is hard to see how pioneering immigrants had such detailed knowledge of the area they were colonizing” (Dennell, 1983: 158) so that they could quickly focus on nutritionally optimal productive taxa. Once established in newly occupied places farmers emphasize more highly productive plant domesticates over others resulting in decreasing equitability across taxa and declining species diversity within the agricultural ecology (Rindos, 1984: 275). For any given intensification of an agroecology system, Rindos noted the tendency for:

> (1) a reduction in the number of species on which people rely for their subsistence, (2) an increase in total crop yield, and (3) autecological convergence among all the crops that are important in the relationship. These interrelated tendencies form the basis for the elaboration and dispersal of agricultural systems. [Rindos, 1984: 268]

The expectation therefore within an evolving agricultural system is for a shift from high to low species diversity in plant domesticates

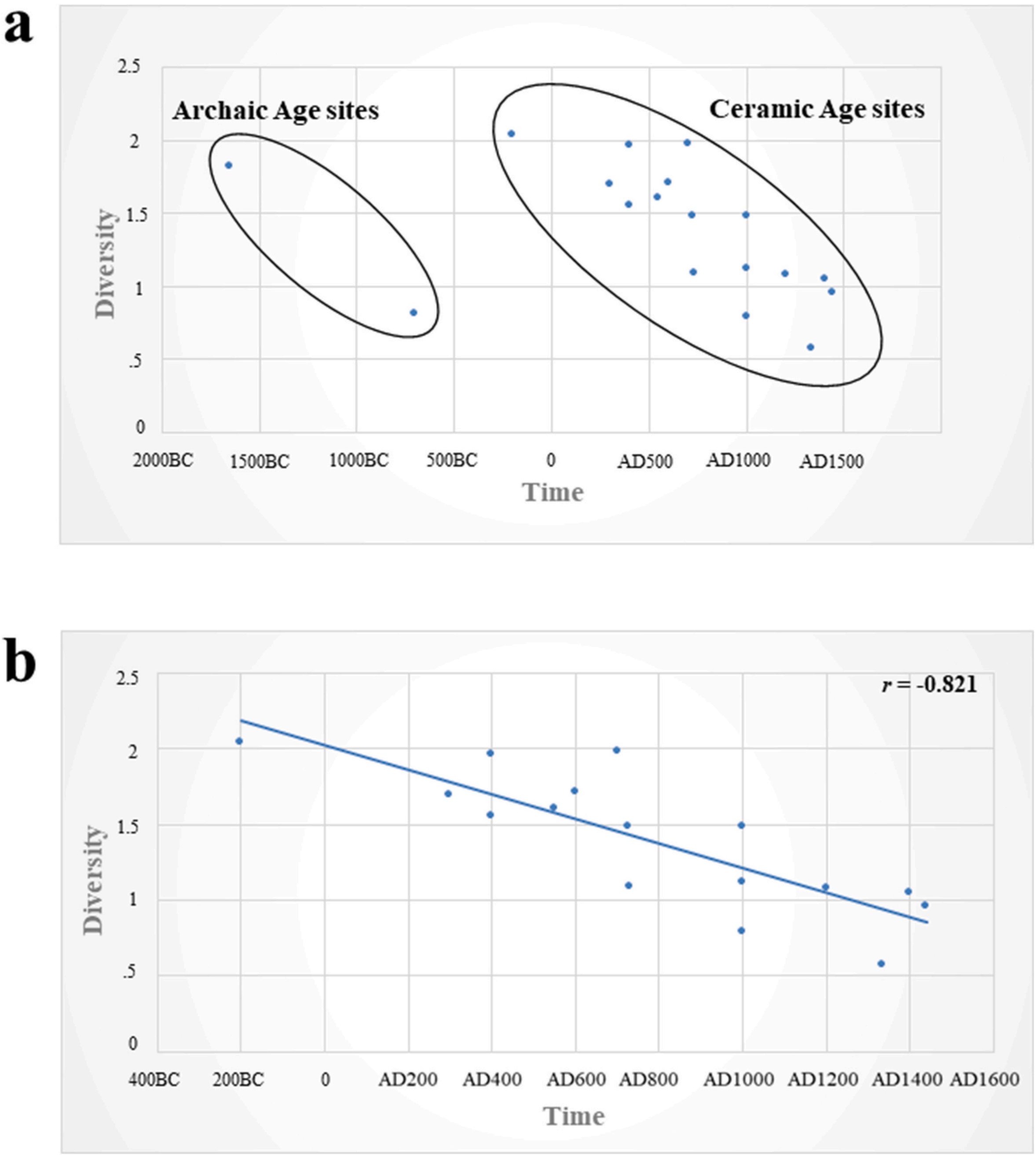


Fig. 6. Plant diversity over time documented in the microbotanical assemblages in Puerto Rico. (a) All sites. With only two Archaic sites, it is difficult to discuss a trend. (b) The Ceramic Age distribution conforms to expectations in human behavioral ecology, agroecology, and agricultural evolution. The Early Ceramic Age sites or site contexts are highest in plant diversity and through time diversity declines as some taxa were emphasized over others. Pearson's product moment correlation coefficient $r = -0.821$.

(Rindos, 1984: 265–271). Documented shifts from high to low ethnobotanical diversity values over time in the Caribbean Ceramic Age are consistent with ideas related to the broad spectrum and diffuse adaptations proposed for early Neolithic populations transitioning from mobile hunter-gatherer-forager to sedentary lifeways, and who were increasingly reliant on plant domesticates (Cleland, 1976; Flannery, 1969; Stiner, 2001).

Following Rindos and in her review of New World agriculture, Pearsall argued that as human-plant relations intensified and evolved, domesticated plants are more prevalent in ethnobotanical assemblages: "the ratio of wild to domestic taxa declines … [and that] agricultural domestication is characterized by declining species diversity" (Pearsall, 1995: 161–162). With the shift to agricultural domestication there may also be geographic expansion of populations and establishment of new settlements (Pearsall, 1995: 162).

The trend in diversity values in the residue data (Table 8) and settlement patterns documented for Puerto Rico generally conform to the expectations outlined by Pearsall. Maruca (Archaic) and the Saladoid/Huecoid contexts were clustered to the higher range of the diversity indexes. Diversity values were considerably lower for the later Ostionoid (post-Saladoid) contexts (Table 8; Fig. 6). The Archaic and Early Saladoid contexts represent first colonizers for two separate colonizing populations, with Archaic groups coming from Central America and Saladoid migrants from South America. Both sets of groups necessarily would have gone through the same or similar processes of landscape learning and agricultural intensification (Fig. 6). The dynamics of the

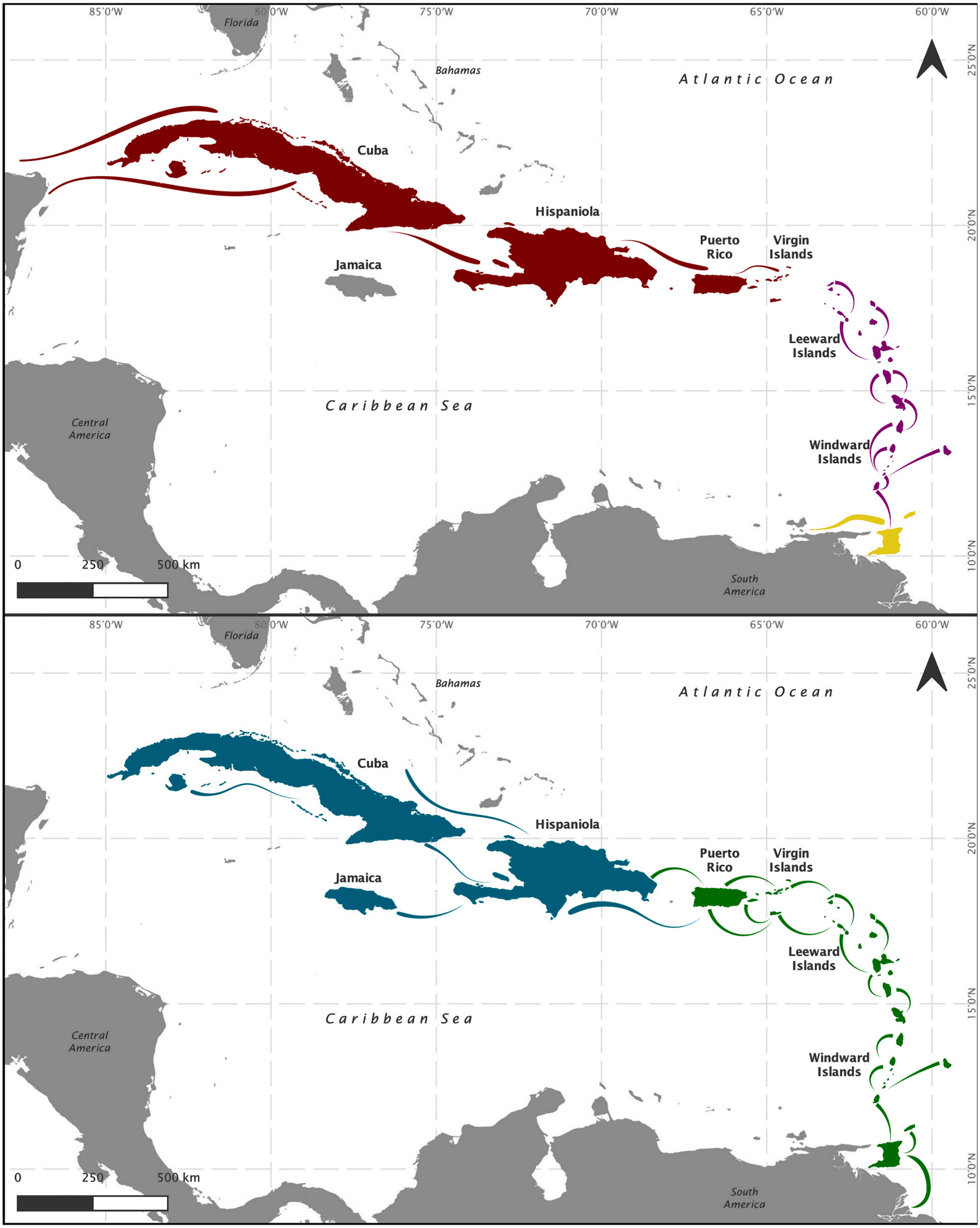


Fig. 7. Maps of the Caribbean showing colonization pulses at different times in prehistory. The upper map shows the initial peopling of (1) the Greater Antilles (except Jamaica) from Central America (c. 4500BC) and (2) Trinidad from South America (c. 6000BC) and continuing into the Lesser Antilles (c. 3000BC). The bottom map shows the Early Ceramic Age colonization of the Lesser Antilles, Puerto Rico, and the eastern tip of Hispaniola (c. 500/700BC) and then the Late Ceramic Age peopling of the Greater Antilles (c. AD500/600). Maps produced by Philip Riris (Bournemouth University) and Howard Wilson.

process certainly would have been different for the two populations; the Archaic people were coming to new landscapes untouched by humans and the Saladoids arrived to islands already occupied and modified for millennia.

There are too few Archaic sites documented for Puerto Rico to address shifts in settlement patterns during the Archaic Age. Most Early Saladoid/Huecoid (c. 300BC–AD400) sites are located on or near a coastline (Siegel, 1991b). By the Late Saladoid (c. AD400–700) and later quite a few more sites are documented for the island. With increasing site frequency, especially in the post-Saladoid periods (c. AD700–1500), a broad range of landforms and habitat types was occupied, including interior montane regions. Geographic expansion of settlements resulted from evolving political organization, the formation of settlement hierarchies, and feuding between increasingly competitive polities (Siegel, 2010, 2011). Major chiefly centers were linked to surrounding smaller hamlets or villages. The decline in diversity of plant taxa is related to political processes as groups narrowed their emphasis on key productive domesticates to support larger populations and organize labor.

7. Concluding remarks

Results of starch and phytolith analyses on artifact samples from Maisabel and HU-7 are consistent with other residue studies from precolonial sites in Puerto Rico with maize dominating the assemblages. Notably, manioc was poorly represented. Plant taxa from the Early Saladoid contexts of Maisabel were considerably more diverse than the post-Saladoid contexts of Maisabel and HU-7. Integrating these findings with other residue studies from Puerto Rico conforms to expectations from human behavioral ecology: overall taxonomic diversity declines with agricultural intensification. Agricultural intensification in Puerto Rico was linked to the evolution of increasingly complex chiefly formations well documented in the archaeological and ethnohistoric records.

Consistent trajectories of diffuse to focal, broad to narrow spectrum, and diverse to less diverse human-plant relations have been documented worldwide, especially in the context of growing populations and increasingly complex political formations. It remains to be seen whether such trends in human-plant (and animal?) relations are sustainable into the future of the planet given massive monocropping and associated impacts of erosion, pollution of hydrological systems from pesticides and fertilizers, and crop failures due to extremes in weather conditions and invasive pest species. In terms of sustainability and human-environmental relations, agronomists, agricultural engineers, and policy makers may conclude that it is beneficial and risk-averse to promote more ecologically diverse farming practices (see Tittonell et al., 2020).

Ecological measures of diversity are well suited to studying the range of plants exploited and their intensity of use geographically and through time. With consistent and replicable sampling designs, a Caribbean regional database of microbotanical identifications and diversity indexes will enable us to develop refined models of plant introductions and in situ trajectories of agricultural and ethnobotanical evolution.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2023.105859.

References

Balée, W., 1988. The Ka'apor Indian wars of lower Amazonia, ca. 1825–1928. In: Randolph, R., Schneider, D., Diaz, M. (Eds.), Dialectics and Gender: Anthropological Approaches. Westview Press, Boulder, pp. 155–169.

Benzoni, G., 2017. In: The History of the New World: Benzoni's Historia del Mondo Nuovo. Byars, J. (Transl.). Pennsylvania State University Press, University Park.

Berman, M.J., Pearsall, D.M., 2000. Plants, people, and culture in the prehistoric central Bahamas: a view from the Three Dog Site, an early Lucayan settlement on San Salvador Island, Bahamas. Lat. Am. Antiq. 11, 219–239.

Berman, M.J., Pearsall, D.M., 2008. At the crossroads: starch grain and phytolith analyses in Lucayan prehistory. Lat. Am. Antiq. 19, 181–203.

Berman, M.J., Pearsall, D.M., 2020. Crop dispersal and Lucayan tool use: investigating the creation of transported landscapes in the central Bahamas through starch grain, phytolith, macrobotanical, and artifact studies. J. Field Archaeol. 45, 355–371.

Burney, D.A., Burney, L.P., MacPhee, R.D.E., 1994. Holocene charcoal stratigraphy from Laguna Tortuguero, Puerto Rico, and the timing of human arrival on the island. J. Archaeol. Sci. 21, 273–281.

Carneiro, R.L., 1981. The chiefdom: precursor of the state. In: Jones, G.D., Kautz, R.R. (Eds.), The Transition to Statehood in the New World. Cambridge University Press, Cambridge, pp. 37–79.

Carneiro, R.L., 1990. Chiefdom-level warfare as exemplified in Fiji and the Cauca Valley. In: Haas, J. (Ed.), The Anthropology of War. Cambridge University Press, Cambridge, pp. 190–211.

Chanlatte Baik, L.A., Narganes Storde, Y.M., 1991. El hombre de Puerto Ferro, Vieques – Puerto Rico. Proc. Congress Int. Assoc. Caribbean Archaeol. 14, 599–611.

Chinique de Armas, Y., Buhay, W. M., Rodríguez Suárez, R., Bestel, S., Smith, D. Mowat, S. D., Roksandic, M., 2015. Starch analysis and isotopic evidence of consumption of cultigens among fisher-gatherers in Cuba: the archaeological site of Canímar Abajo, Matanzas. J. Archaeol. Sci. 58, 121–132.

Ciofalo, A.J., Keegan, W.F., Pateman, M.P., Pagán-Jiménez, J.R., Hofman, C.L., 2018. Determining precolonial botanical foodways: starch recovery and analysis, Long Island, The Bahamas. J. Archaeol. Sci.: Rep. 21, 305–317.

Ciofalo, A.J., Sinelli, P.T., Hofman, C.L., 2019. Late precolonial culinary practices: starch analysis on griddles from the northern Caribbean. J. Archaeol. Method and Theory 26, 1632–1664.

Cleland, C.E., 1976. The focal-diffuse model: an evolutionary perspective on the prehistoric cultural adaptations of the eastern United States. Midcont. J. Archaeol. 1 (1), 59–76.

Colón, F., 1959. The Life of the Admiral by His Son, Ferdinand. Keen, B. (Transl.). Rutgers University Press, New Brunswick.

Curet, L.A., 2005. Caribbean Paleodemography: Population, Culture History, and Sociopolitical Process in Ancient Puerto Rico. University of Alabama Press, Tuscaloosa.

DeBoer, W.R., 1975. The archaeological evidence for manioc cultivation: a cautionary note. Am. Antiq. 40, 419–433.

Dennell, R., 1983. European Economic Prehistory: A New Approach. Academic Press, London.

Diehl, M.W., 2017. Paleoethnobotanical sampling adequacy and ubiquity: an example from the American Southwest. Adv. Archaeol. Prac. 5 (2), 1–10.

Dunn, O., Kelley Jr., J.E., 1989. The *Diario* of Christopher Columbus's First Voyage to America 1492–1493. University of Oklahoma Press, Norman.

Espenshade, C.T., Newsom, L., Duncan, N.A., Pearsall, D.M., Jones, J.G., 2014. The Cultural Landscape of Jácana: Archaeological Investigations at Site PO-29, Municipio de Ponce, Puerto Rico. Volume II, Part 8: Paleoethnobotany of Jácana.

New South Associates, Stone Mountain, Georgia. Submitted to U. S. Army Corps of Engineers, Jacksonville District, Jacksonville, Florida.

Farahani, A., Sinensky, R.J., 2022. Challenges and prospects of richness and diversity measures in paleoethnobotany. In: Eren, M.I., Briggs, B. (Eds.), Defining and Measuring Diversity in Archaeology: Another Step toward an Evolutionary Synthesis of Culture. Berghahn, New York, pp. 178–212.

Ferguson, R.B., 1990. Explaining war. In: Haas, J. (Ed.), The Anthropology of War. Cambridge University Press, Cambridge, pp. 26–55.

Flannery, K., 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P.J., Dimbleby, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Aldine, Chicago, pp. 73–100.

Hinkle, D.E., Wiersma, W., Jurs, J.G., 2003. Applied Statistics for the Behavioral Sciences, 5th ed. Houghton Mifflin, Boston.

Hofman, C.L., Bright, A.J., Boomert, A., Knippenberg, S., 2007. Island rhythms: the web of social relationships and interaction networks in the Lesser Antillean archipelago between 400 B.C. and A.D. 1492. Lat. Am. Antiq. 18, 243–268.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Huston, M.A., 1994. Biological Diversity: the Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

Hutchinson, G.E., 1967. A Treatise on Limnology, Volume II: Introduction to Lake Biology and the Limnoplankton. John Wiley, New York.

Keegan, W.F., Hofman, C.L., 2017. The Caribbean before Columbus. Oxford University Press, New York.

Kirch, P.V., 1984. The Evolution of the Polynesian Chiefdoms. Cambridge University Press, Cambridge.

Kirch, P.V., 1990. The evolution of sociopolitical complexity in prehistoric Hawaii: an assessment of the archaeological evidence. J. World PreHistory 4, 311–345.

Las Casas, B. de, 1951. Historia de las Indias. Fondo de Cultura Economica, México, D.F.

Lathrap, D.W., 1970. The Upper Amazon. Thames and Hudson, London.

Magurran, A.E., McGill, B.J. (Eds.), 2011. Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford.

Mickelburgh, H.L., Pagán-Jiménez, J.R., 2012. New insights into the consumption of maize and other food plants in the pre-Columbian Caribbean from starch grains trapped in human dental calculus. J. Archaeol. Sci. 39, 2468–2478.

Moscoso, F., 1981. The Development of Tribal Society in the Caribbean. PhD dissertation. State University of New York at Binghamton. University Microfilms, Ann Arbor.

Netting, R., 1974. Functions of war. Man 9, 485–487.

Newsom, L.A., Pearsall, D.M., 2003. Temporal and spatial trends indicated by a survey of archaeobotanical data from the Caribbean islands. In: Minnis, P. (Ed.), People and Plants in Ancient North America 1: East. Smithsonian Institution Press, Washington, D.C., pp. 347–412

Newsom, L.A., Wing, E.S., 2004. On Land and Sea: Native American Uses of Biological Resources in the West Indies. University of Alabama Press, Tuscaloosa.

Oviedo, G. F. de, 1959. Natural History of the West Indies. Stoudemire, S. (Transl.). University of North Carolina Press, Chapel Hill.

Pagán-Jiménez, J.R., 2007. De antiguos pueblos y culturas botánicas en el Puerto Rico indígena: el archipiélago borincano y la llegada de los primeros pobladores agroceramistas. In: BAR International Series, 1687. Archaeopress, Oxford.

Pagán-Jiménez, J.R., 2008. Envisioning ancient human plant use at the Río Tanamá Site 2 (AR-39) through starch analysis of lithic and clay griddle implements. In: Carlson, L.A. (Ed.), A Multidisciplinary Approach to Site Testing and Date Recovery at Two Village Sites (AR-38 and AR-39) on the Lower Río Tanamá, Municipality of Arecibo, Puerto Rico. Submitted to U.S. Army Corps of Engineers, Jacksonville District, Jacksonville, Florida. Southeastern Archaeological Research, Inc., Orlando, Florida, pp. 241–257.

Pagán-Jiménez, J.R., 2009. Nuevas perspectivas sobre las culturas botánicas precolombinas de Puerto Rico: implicaciones del studio de almidones en herramientas líticas, cerámicas y de concha. Cuba Arqueológica II (2), 7–23.

Pagán-Jiménez, J.R., 2011a. Early phytocultural processes in the precolonial Antilles: a pan-Caribbean survey for an ongoing starch grain research. In: Hofman, C.L., van Duijvenbode, A. (Eds.), Communities in Contact: Essays in Archaeology, Ethnohistory and Ethnography of the Amerindian Circum-Caribbean. Sidestone Press, Leiden, pp. 87–116.

Pagán-Jiménez, J.R., 2011b. Assessing ethnobotanical dynamics at CE-11 and CE-33 through analysis of starch grains, plant processing, and cooking artifacts. In: Carlson, L.A., Torres, J. (Eds.), Phase III Data Recovery Investigations at Three Prehistoric Archaeological Sites (CE-11, CE-32, and CE-33), Municipality of Ceiba, Naval Activity Puerto Rico. Submitted to Naval Facilities Engineering Command Southeast, Norfolk, Virginia. Southeastern Archaeological Research, Inc., Orlando, Florida, pp. 325–374.

Pagán-Jiménez, J.R., 2011c. Dinámicas fitoculturales de un pueblo precolombino saladoide tardío (King's Helmet) en Yabucoa, Puerto Rico. El Caribe Arqueológico 12, 45–59.

Pagán-Jiménez, J.R., 2013. Human-plant dynamics in the precolonial Antilles: a synthetic update. In: Keegan, W.F., Hofman, C.L., Rodríguez Ramos, R. (Eds.), The Oxford Handbook of Caribbean Archaeology. Oxford University Press, New York, pp. 391–406.

Pagán-Jiménez, J.R., 2022. Zamia in the insular Caribbean: new insights into the historical ecology of an ancient wild food plant. In: Carrasco, M.D., Cibrián-Jaramillo, A., Bonta, M.A., Englehardt, J.D. (Eds.), Under the Shade of Thipaak: the Ethnoecology of Cycads in Mesoamerica and the Caribbean. University Press of Florida, Gainesville, pp. 97–124.

Pagán-Jiménez, J.R., Carlson, L.A., 2014. Recent archaeobotanical findings of the hallucinogenic snuff cojoba (*Anadenanthera peregrina* (L.) Speg.) in precolonial Puerto Rico. Lat. Am. Antiq. 25, 101–116.

Pagán-Jiménez, J.R., Mickleburgh, H.L., 2023. Caribbean deep-time culinary worlds revealed by ancient food starches: beyond the dominant narratives. J. Archaeol. Res. 31, 55–101.

Pagán-Jiménez, J.R., Oliver, J.R., 2008. Starch residues on lithic artifacts from two contrasting contexts in northwestern Puerto Rico: los Muertos Cave and Vega de Nelo Vargas Farmstead. In: Hofman, C.L., Hoogland, M.L.P., van Gijn, A.L. (Eds.), Crossing the Borders: New Methods and Techniques in the Study of Archaeological Materials from the Caribbean. University of Alabama Press, Tuscaloosa, pp. 137–158.

Pagán-Jiménez, J.R., Rodríguez López, M.A., Chanlatte Baik, L.A., Narganes Storde, Y., 2005. La temprana introducción y uso de algunas plantas domésticas, silvestres y cultivos en Las Antillas precolombinas: una primera revaloración desde la perspectiva del "arcaico" de Vieques y Puerto Rico. Diálogo Antropológico 3 (10), 7–33.

Pagán-Jiménez, J.R., Rodríguez Ramos, R., Reid, B.A., van den Bel, M., Hofman, C.L., 2015. Early dispersals of maize and other food plants into the southern Caribbean and northeastern South America. Quat. Sci. Rev. 123, 231–246.

Pearsall, D.M., 1995. Domestication and agriculture in the new World tropics. In: Price, T.D., Gebauer, A.B. (Eds.), Last Hunters, First Farmers: New Perspectives on the Prehistoric Transition to Agriculture. School of American Research Press, Santa Fe, New Mexico, pp. 157–192.

Pearsall, D.M., 2009. Investigating the transition to agriculture. Curr. Anthropol. 50, 609–613.

Pearsall, D.M., 2015. Paleoethnobotany: A Handbook of Procedures, 3. Routledge, New York.

Pearsall, D.M., Duncan, N.A., Chandler-Ezell, K., Ubelaker, D.H., Zeidler, J.A., 2020. Food and society at Real Alto, an early Formative community in southwest coastal Ecuador. Lat. Am. Antiq. 31, 122–142.

Perry, L., 2002. Starch analyses reveal multiple functions of quartz "manioc" grater flakes from the Orinoco Basin. Venezuela. Interciencia 27, 635–639.

Perry, L., 2005. Reassessing the traditional interpretation of "manioc" artifacts in the Orinoco Valley of Venezuela. Lat. Am. Antiq. 16, 409–426.

Pestle, W.J., Perez, E.M., Koski-Karell, D., 2023. Reconsidering the lives of the earliest Puerto Ricans: mortuary archaeology and bioarchaeology of the Ortiz Site. PLoS One 18 (4). https://doi.org/10.1371/journal.pone.0284291.

Pielou, E.C., 1975. Ecological Diversity. John Wiley, New York.

Pielou, E.C., 1977. Mathematical Ecology, 2. John Wiley, New York.

Piperno, D.R., Pearsall, D.M., 1998. The Origins of Agriculture in the Lowland Neotropics. Academic Press, San Diego.

Piperno, D., Ranere, A.J., Holst, I., Hansell, P., 2000. Starch grains reveal early root crop horticulture in the Panamanian tropical forest. Nature 407 (6806), 894–897.

Rindos, D., 1984. The Origins of Agriculture: an Evolutionary Perspective. Academic Press, Orlando.

Rivera-Collazo, I.C., 2015. *Por el camino verde*: long-term tropical socioecosystem dynamics and the Anthropocene as seen from Puerto Rico. Holocene 25, 1604–1611.

Rockman, M., Steele, J., 2003. Colonization of Unfamiliar Landscapes: the Archaeology of Adaptation. Routledge, London.

Rodríguez, M., 1999. Excavations at Maruca, a preceramic site in southern Puerto Rico. Proc. Congress Int. Assoc. Caribbean Archaeol. 17, 166–180.

Rodríguez Ramos, R.R., Pagán-Jiménez, J., 2006. Interacciones multivectoriales en el Circum-Caribe precolonial: un vistazo desde las antillas. Caribb. Stud. 34 (2), 103–143.

Rodríguez Ramos, R., Rodríguez López, M., Pestle, W.J., 2023. Revision of the cultural chronology of precolonial Puerto Rico: a Bayesian approach. PLoS One 18 (2), e0282052. https://doi.org/10.1371/journal.pone.0282052.

Roe, P.G., 1989. A grammatical analysis of Cedrosan Saladoid vessel form categories and surface decoration aesthetic and technical styles in early Antillean ceramics. In: Siegel, P.E. (Ed.), Early Ceramic Population Lifeways and Adaptive Strategies in the Caribbean. BAR International Series 506. British Archaeological Reports, Oxford, pp. 267–382.

Rouse, I., 1948. The Arawak. In: Steward, J.H. (Ed.), Handbook of South American Indians, The Circum-Caribbean Tribes. Bureau of American Ethnology Bulletin 143, vol. 4. Smithsonian Institution, Washington D. C., pp. 507–546

Rouse, I., 1992. The Tainos: Rise and Decline of the People Who Greeted Columbus. Yale University Press, New Haven.

Sauer, C.O., 1966. The Early Spanish Main. University of California Press, Berkeley.

Schulting, R.J., Snoeck, C., Pouncett, J., Brock, F., Bronk Ramsey, C., Higham, T., Devièse, T., Delancy, K., Pateman, M., Keegan, W., Ostapkowicz, J., 2021. Six centuries of adaptation to a challenging island environment: AMS ^{14}C dating and stable isotopic analysis of pre-Columbian human remains from the Bahamian archipelago reveal dietary trends. Quat. Sci. Rev. 254 https://doi.org/10.1016/j.quascirev.2020.106780.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana.

Siegel, P.E., 1989 (Ed.). In: Early Ceramic Population Lifeways and Adaptive Strategies in the Caribbean. British Archaeological Reports, Oxford. BAR International Series 506.

Siegel, P.E., 1991a. Migration research in Saladoid archaeology: a review. Fla. Anthropol. 44 (1), 79–91.

Siegel, P.E., 1991b. Saladoid survival strategies: evidence from site locations. Proc. Congress Int. Assoc. Caribbean Archaeol. 14, 315–337.

Siegel, P.E., 1992. Ideology, Power, and Social Complexity in Prehistoric Puerto Rico. PhD dissertation,State. University of New York at Binghamton. University Microfilms, Ann Arbor.

Siegel, P.E., 1995. The archaeology of community organization in the tropical lowlands: a case study from Puerto Rico. In: Stahl, P.W. (Ed.), Archaeology in the American

Tropics: Current Analytical Methods and Applications. Cambridge University Press, Cambridge, pp. 42–65.

Siegel, P.E., 1996. Ideology and culture change in prehistoric Puerto Rico: a view from the community. J. Field Archaeol. 23, 313–333.

Siegel, P.E., 2002. Archaeological Data Recoveries at Sites HU-6 and HU-7, Río Antón Ruíz Flood Control Project, Municipio de Humacao, Puerto Rico. Submitted to U. S. Army Corps of Engineers, Jacksonville District. New South Associates, Stone Mountain, Georgia.

Siegel, P.E., 2004. What happened after AD 600 in Puerto Rico? Corporate groups, population restructuring, and post-Saladoid social changes. In: Delpuech, A., Hofman, C.L. (Eds.), Late Ceramic Age Societies in the Eastern Caribbean. BAR International Series 1273, Oxford, England, pp. 87–100.

Siegel, P.E., 2010. Continuity and change in the evolution of religion and political organization on pre-Columbian Puerto Rico. J. Anthropol. Archaeol. 29, 302–326.

Siegel, P.E., 2011. Competitive polities and territorial expansion in the Caribbean. In: Curet, L.A., Hauser, M.W. (Eds.), Islands at the Crossroads: Migration, Seafaring, and Interaction in the Caribbean. University of Alabama Press, Tuscaloosa, pp. 193–218.

Siegel, P.E., 2018 (Ed.). Island Historical Ecology: Socionatural Landscapes of the Eastern and Southern Caribbean. Berghahn, New York.

Siegel, P.E., Jones, J.G., Pearsall, D.M., Wagner, D.P., 2005. Environmental and cultural correlates in the West Indies: a view from Puerto Rico. In: Siegel, P.E. (Ed.), Ancient Borinquen: Archaeology and Ethnohistory of Native Puerto Rico. University of Alabama Press, Tuscaloosa, pp. 88–121.

Siegel, P.E., Jones, J.G., Pearsall, D.M., Dunning, N.P., Farrell, P., Duncan, N.A., Curtis, J. H., Singh, S.K., 2015. Paleoenvironmental evidence for first human colonization of the eastern Caribbean. Quat. Sci. Rev. 129, 275–295.

Smith, B.D., 2001. Low-level food production. J. Archaeol. Res. 9, 1–43.

Stiling, P., 1999. Ecology: Theories and Applications, 3. Prentice Hall, Upper Saddle River, New Jersey.

Stiner, M.C., 2001. Thirty years on the “Broad Spectrum Revolution" and paleolithic demography. Proc. Natl. Acad. Sci. USA 98 (13), 6993–6996.

Sturtevant, W.C., 1961. Taino agriculture. In: Wilbert, J. (Ed.), The Evolution of Horticultural Systems in Native South America: Causes and Consequences. Sociedad de Ciencias Naturales la Salle, Caracas, pp. 69–82. Antropologica Supplement Publication 2.

Sturtevant, W.C., 1969. History and ethnography of some West Indian starches. In: Ucko, P.J., Dimbleday, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Aldine, Chicago, pp. 177–199.

Tittonell, P., Piñeiro, G., Garibaldi, L.A., Dogliotti, S., Olff, H., Jobbagy, E.G., 2020. Agroecology in large scale farming — a research agenda. Front. Sustain. Food Syst. 4, 584605 https://doi.org/10.3389/fsufs.2020.584605.

Wilson, S.M., 2007. The Archaeology of the Caribbean. Cambridge University Press, New York.

Wilson, S.M., Iceland, H.B., Hester, T.R., 1998. Preceramic connections between Yucatán and the Caribbean. Lat. Am. Antiq. 9, 342–352.

Yde, J., 1965. Material Culture of the Waiwái. Nationalmuseets Skrifter Etnografisk Række X. The National Museum of Copenhagen, Copenhagen.