

The phytoliths of Naachtun (Petén, Guatemala): Development of a modern reference for the characterization of plant communities in the Maya Tropical Lowlands

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Abstract:

Phytoliths, unlike pollen and charcoal, are frequently conserved in sediments in the Maya lowlands but are rarely used as paleoenvironmental proxies. To better interpret and reconstruct paleoecological signatures and changes, it is necessary to provide current analogues of fossil assemblages. To do so, we selected six modern ecosystems and differentiated them by their soil phytolith assemblages in the ancient Maya city of Naachtun (northern Petén, Guatemala). We studied the plant communities and relative phytoliths frequencies in surface soils on four north-south vegetation transect, composed of 43 quadrats. These transects cross forests and savannahs in low swampy areas North and South of the site, and hill forest in its center, where the city was built. Quadrats were statistically compared using multivariate analyses (CA). Six types of plant communities were characterized by their phytolith assemblages, as well as on the presence of siliceous bioindicators such as diatoms and sponges. The D/P and LU indexes developed for these assemblages allow us to provide a precise signature of the current vegetation cover, and identify the presence of undergrowth in forest areas, or forest edges in savannah areas. This first modern phytolith reference for the Maya area will contribute to the development of paleoecological reconstructions for this zone.

1	The phytoliths of Naachtun (Petén, Guatemala): Development of a modern reference for the
2	characterization of plant communities in the Maya Tropical Lowlands
3	
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21	Highlights
22	
23	- Botanical description of 6 plant communities in the Petén
24	- Distinction and identification of ecosystems through phytolith assemblages
25	- Use of phytolith indices to specify the ecology of plant formations
26	- First modern environmental reference for phytoliths in the Maya lowlands
27	

Phytoliths, unlike pollen and charcoal, are frequently conserved in sediments in the Maya lowlands 30 but are rarely used as paleoenvironmental proxies. To better interpret and reconstruct 31 paleoecological signatures and changes, it is necessary to provide current analogues of fossil 32 assemblages. To do so, we selected six modern ecosystems and differentiated them by their soil 33 phytolith assemblages in the ancient Maya city of Naachtun (northern Petén, Guatemala). We 34 studied the plant communities and relative phytoliths frequencies in surface soils on four north-35 36 south vegetation transect, composed of 43 quadrats. These transects cross forests and savannahs in low swampy areas North and South of the site, and hill forest in its center, where the city was built. 37 Quadrats were statistically compared using multivariate analyses (CA). Six types of plant 38 communities were characterized by their phytolith assemblages, as well as on the presence of 39 siliceous bioindicators such as diatoms and sponges. The D/P and LU indexes developed for these 40 41 assemblages allow us to provide a precise signature of the current vegetation cover, and identify the presence of undergrowth in forest areas, or forest edges in savannah areas. This first modern 42 phytolith reference for the Maya area will contribute to the development of paleoecological 43 44 reconstructions for this zone.

45

46 Keywords

47

Phytoliths assemblages; Naachtun; Maya Lowland, Petén forests; *Sival* wetland; phytolith indexes

50 1. Introduction

51

Today, while more and more studies are focusing on the systemic collapse of our modern civilization (Meadows et al., 2004; Erhlich and Ehrlich, 2013; Servigne and Stevens, 2015), some are interested in ancient societies that have disappeared as a way of addressing modern social or 55 environmental crises (Tainter, 1988; Diamond, 2005). The Maya societies of the Yucatán Lowland, well known for their huge architectural remains, are a good example. Studies testify to two major 56 collapse events that occurred in the 2nd century (pre-classical collapse) and the 10th century 57 (classical collapse) CE. While these collapse events are sometimes presented as the result of overly 58 intensive environmental exploitation (Abrams and Rue, 1988; Hansen et al. 2002; Lentz and 59 Hockaday, 2009; Turner and Sabloff, 2012), other authors question this hypothesis by citing the 60 Maya's considered and sustainable management of forest and plant resources (Fedick, 2010; 61 Mcneil, 2012; Lentz et al., 2015; Thompson et al., 2015). 62

63 Located in the extreme north of Guatemala (Fig. 1), four kilometers from the border with Campeche (Mexico), the archaeological site of Naachtun was first surveyed in 1922, by SG. 64 Morley, and 10 years later by CL. Lundell (Lundell, 1932). Since 2000, Naachtun has been the site 65 of archaeological and palaeoenvironmental studies (Reese-Taylor et al., 2005; Nondédéo et al., 66 2012; 2013) and is also one of the location of the Lidar project, which aims to map the geographical 67 68 and archaeological characteristics of Maya sites in northern Guatemala (Canuto et al., 2018). Given its well-preserved monumental remains, the site holds a certain archaeological interest. Indeed, the 69 70 first archaeological evidence of occupation dates to the 5th century BCE, although the development 71 of the city only began in earnest in the 1st century CE; that is, at around the time of the pre-classical period Maya collapse (Hansen et al., 2002). Located halfway between Tikal and Calakmul, the two 72 great Maya kingdoms of Petén during the classical period, Naachtun played the role of a regional 73 74 political center and may have counted several thousand inhabitants. The site was eventually abandoned around 950 CE, relatively late period in comparison to the other capitals of the Petén 75 region (Nondédéo et al., 2013). 76

In order to understand the link between past cultural and environmental changes, this study uses both the archaeological context and geomorphological/palaeoenvironmental context. Naachtun is located on a large hilly escarp and is bordered to the north and south by two depressions of the karstic polje type (Castanet et al. 2016), called *bajos*, with dispersed perennial wetlands, locally called *Sival* (Fig. 2). During the wet season, these *Sival* are fed by water and result in considerable

82 palustrine-alluvial sedimentation. These sedimentary sequences located in the northern *bajo* cover

83 the periods of occupation of the Naachtun site and create a good trap for the bioindicators

84 (phytoliths, mollusks, etc.) used for palaeoenvironmental reconstructions.

In the Maya Lowlands, most bio-proxies used in palaeoenvironmental studies to reconstruct 85 past vegetation dynamics are either pollen (Islebe, 1996; Levden, 2002; Carozza et al., 2007; Wahl 86 et al., 2006; 2013) or charcoal (Lentz and Hockabay, 2009; Lentz, 2015; Dussol et al., 2017). 87 However, in Naachtun's *bajo* records, pollen are poorly preserved, while the identifiable charcoals 88 are too diluted to allow for systematic study. This poor conservation led us to look for new 89 90 bioindicators of past vegetation changes. Due to their siliceous structure, phytoliths are resistant to oxidation and are well preserved in such tropical environment deposits (Alexandre, et al., 1997; 91 Madella and Lancelotti, 2012; Piperno, 2006; Watling et al., 2016). They also allow good 92 monitoring of herbaceous environments thanks to the morphotype diversity of Cyperaceae and 93 Poaceae (Twiss et al., 1969; Fredlund and Tieszen, 1994; Lu and Liu, 2003; Stromberg, 2004, 94 95 Iriarte and Paz, 2009; Novello et al., 2012). Moreover, unlike pollen, phytoliths are a good local bioindicator of plant formations (Madella and Lancelotti, 2012; Piperno, 2006). However, in the 96 Maya zone, research involving phytoliths is scarce and has been conducted using only a few 97 98 particular morphotypes (Beach et al., 2009), or in specific archaeological contexts (Bozart and 99 Guderjan, 2004; Abramiuk et al., 2011).

Given the lack of phytolith studies in this forest region, it is difficult to interpret fossil assemblages in the sedimentary archives. The main problem in forest environments is that phytoliths do not allow for taxonomic discrimination between woody dicotyledons (Alexandre et al., 1997; Piperno, 2006; Mercader et al., 2009; Collura and Neumann, 2017). However, in similar environments of tropical lowland forests, like the Amazon rainforest, recent studies have pointed to the possibility of characterizing the different forest ecosystems by studying phytolith assemblages (Dickau et al., 2013; Watling et al., 2016).

107 The aim of this study is, therefore, to assess the potential of phytoliths in the Maya108 Lowlands to serve as a good proxy of plant formations. To achieve this purpose, a botanical study

109 has been carried out on 43 ecological quadrats located along four transects crossing the different ecosystems of the Naachtun site. For each quadrat, surface soils were sampled and phytolith 110 assemblages analyzed using the general counting and index approaches. The link between phytolith 111 assemblages and plant communities was tested using a distribution diagram, and also a statistical 112 study using a component analysis. In this paper, we will compare the different phytolith indexes and 113 propose a new index to better establish the landscape characteristics of these communities. 114 115 2. Study Area 116 117 2.1. Climate and geology 118 119 The department of Petén is located in the southern part of the Petén tropical forest covering 120 the central lowlands of the Yucatán peninsula, also referred as the Maya Lowlands (Fig. 1). The 121 vegetation of Petén is mainly subject to two control factors: precipitations and regional 122 geomorphology (Sánchez-Sánchez and Islebe, 2002; Carrilo-Bastos et al., 2012). Indeed, seasonal 123 latitudinal migrations of the Inter-Tropical Convergence Zone (ITCZ) and the North Atlantic High 124 125 cause considerable seasonality of precipitation (Hastenrath, 1976; 1984; Brenner et al., 2001; 126 Hodell et al., 2005; Carrillo-Bastos et al., 2012). Thus, most of the rainfall, between 1,000 and 1,500 mm, is concentrated in the period from May to December, while the period from January to 127 128 April corresponds to a dry season. Due to the intertropical position of the peninsula, temperatures remain relatively stable throughout the year (Wilson, 1980). These umbrothermal conditions 129 correspond to an Am-type climate in the Köppen classification (Pennington and Sarukhán, 2005). 130 The regional geomorphology of Petén is a vast Meso-Cenozoic carbonate platform, composed 131 mainly of limestone, at low altitude (250–300 m). The fractures and heterogeneities of the limestone 132 bedrock have produced karstified landscapes resulting in hills alternating with depressions (bajos) 133 (Dunning et al., 2002; Beach et al., 2008, 2009). Consequently, differences in hydrology and soil 134

- composition are also observed, with thin layers of well-drained rendosol on hill and slope areas, and
 seasonally waterlogged vertisol-histosol in *bajo* areas (Beach et al., 2008).
- 137
- 138 2.2. The plant formations of Petén
- 139

The Petén forest was first described in the 1930s by Lundell (1937) and was defined as a 140 semi-sempervirent tropical forest. However, this ecological classification does not reflect the true 141 diversity of forest ecosystems found in the different geomorphological contexts of Petén. The hill 142 143 zones are covered by high semi-evergreen forests (30–40 m) with calcareous plant associations. The 144 wide trees, characteristic of these forests, belong mostly to the Burseraceae, Fabaceae, Meliaceae, Moraceae, Sapindaceae, and Sapotaceae. The relatively sparse undergrowth is occupied by 145 Arecaceae and Piperaceae shrubs, and a small number of grassy plants. The bajo areas are covered 146 by a low forest (5–8 m), where plant associations are adapted to clayey soils and the seasonal 147 148 submersions and drying periods. These are mainly composed of species belonging to the Anacardiaceae, Euphorbiaceae, Fabaceae and Myrtaceae families. The *bajo* forest undergrowth is 149 150 relatively bare, with very few grasses. In addition to these two main forest ecosystems, it is possible 151 to find other vegetation types, such as palm forests, pine forests, or humid or dry savannahs, 152 adapted to local geomorphological conditions (Lundell, 1937; Martínez and Galindo-Leal, 2002; Schulze and Whitacre, 1999). Currently, the Petén forests are less populated than during the Maya 153 154 period (Canuto et al., 2018). 155

- 156 3. Methodology
- 157

158 3.1. Vegetation study and soil sampling

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160 The vegetation study was conducted during two fieldwork sessions at the end of the dry161 season in March 2016 and April 2017. We have conducted ecological transects crossing all altitude

162 and humidity domains. Thus, we defined three north-south oriented transects in the north bajo area (T1, T2, and T3), and one north-south/west oriented transect (T4), over distances of about one 163 kilometer. These transects therefore covered different plant formations of forests and herbaceous 164 areas from hills and *bajo* (Fig. 2). Along these transects, we identified areas where plant 165 communities were changing. Depending on the extent of a plant community, one to two blocks. 166 each of about 100m², have been positioned in the middle of it. On each quadrat, we recorded the 167 plant species presences based on local common names and annotated their relative quantity. 168 Vegetation cover values were estimated from colorimetric processing (light rate [light-white pixels] 169 170 relative to vegetation coverage rate [dark pixels]) of forest cover photographs taken vertically and to up. Finally, for the phytolith analysis, only a few grams of the surface portion of the A1 horizon 171 (the A0 litter having been removed from the sample) were taken from several locations in each of 172 the quadrat. All samples were mixed to create a single sample of approximately 100 g by quadrat. It 173 allowed us to prevent our sampling producing ultra-local biases in phytolith assemblages. 174

175

The ecological survey was carried out with the help of a local forester able to identify the 176 plants by their vernacular names in Spanish and/or Mayan. The vernacular names were then 177 178 translated into scientific names using the available literature and databases (Lundell, 1937; Standley 179 and Steyermark, 1946; Schulze and Whitacre, 1999; Martínez and Galindo-Leal, 2002; Atran et al., 2004), while some plant specimens were compared with taxonomic types from the Paris Herbarium 180 181 in France's National Museum of Natural History (MNHN). However, the local nomenclature of Naachtun plants contains many synonymies (one local name = different taxa) or polynomials 182 (several local names = one taxon). To resolve this issue, we chose to apply taxonomic corrections, 183 such as the following: 184

- Multiplication of nomen: *zakate* is used to designate both *Kyllinga pumila*, a Cyperaceae,
and *Olyra latifolia*, a Poaceae. In these cases, the vernacular name, nomen, was used several times,
to allow for better taxonomic and ecological representativeness.

188 - Construction of species complex: Manilkara chicle, Pouteria glomerata, Pouteria reticulata, Sideroxylon tepicense, trees belonging to the Sapotaceae family, are all named zapote or 189 *zapotillo*. In such cases, we decided to group all these scientific names under the nomen *zapote*. 190 Phytoliths do not allow for differentiation between woody dicotyledon species. We, therefore, chose 191 to create species complexes for trees (62 nomens associated with woody dicotyledons). Phytoliths 192 are, however, a good tool for characterizing monocotyledon families, such as Arecaceae, 193 Cyperaceae, Commelinaceae, Musaceae, and Poaceae (Piperno, 2006; Honaine et al., 2009; 194 Eichhorn et al., 2010; Novello et al., 2012; Chen and Smith, 2013). With some families, it is 195 196 sometimes possible to determine the genus or species. Thus, for herbaceous plants, we multiplied 197 the nomens to allow for better ecological monitoring using phytoliths (18 nomens). Finally, from the 157 initial occurrences, 75 nomens were assigned to a genus and five nomens to a family (See 198 Table 3 in appendix). It should be noted that these sampling and identification methods were 199 designed to be used primarily on ecological rather than taxonomic assemblages. 200 201 Plant associations were studied by quadrat using a statistical study of nomen occurrences. Each nomen class selected was classified for each of the quadrats based on the following criteria: 202 203 Absent (0 occurrences), Present (1 to 8 occurrences) or Abundant (> 8 occurrences) (Table 3). 204 These occurrence data (coded 0, 1 and 2 respectively) were studied using a hierarchical bottom-up classification coupled with a factor analysis of the correspondences. This statistical methodology 205 aimed to verify the representativeness of the assemblages across the site and compare them with the 206

literature (Lundell, 1937; Schulze and Whitacre, 1999; Martínez and Galindo-Leal, 2002).

208

209 3.2. Preparation and counting of phytolithes

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The procedure for phytolith extraction was adapted from Piperno (2006). For approximately 20 g of soil: (1) Organic Matter was destroyed using hydrogen peroxide (H_2O_2), (2) clays were 213 deflocculated using sodium hexametaphosphate (SHMP; 40 g/L), (3) sand and gravel were removed 214 by sieving at 250 µm, (4) clays were eliminated by draining, and (5) amorphous siliceous matter 215 was concentrated and extracted by densimetric sorting using sodium polytungstate diluted to a

216 density of 2.30–2.35.

The dried residue was mounted on microscope slides in immersion oil to allow rotation and 217 3-D analysis. Observations, identifications, and counts were performed under a microscope at 218 magnifications between x450 and x630. As counting methods influence the ecological interpretation 219 of phytolith assemblages, we followed recommendations in counting at least 200 diagnostic 220 phytolith morphotypes for each sample (Stomberg, 2009; Zurro, 2017). In addition to these 221 diagnostic phytoliths, we also counted non-diagnostic phytolith morphotypes, sponge spicules, and 222 223 diatoms. The results are presented in a diagram of the relative abundances of diagnostic morphotypes. The diagram also includes the relative abundances of non-diagnostic shapes and 224 bioindicators, calculated as the total sum of all particles counted. 225

226

227 3.3. Classification of phytolithes

228

Although phytolith assemblages in the forests of Petén have not yet been studied, other 229 forests in intertropical zones have been the subject of studies, such as those from Amazonia 230 (Piperno 1988; Dickau et al. 2013; Watling et al. 2016), Africa (Alexandre et al, 1997; Barboni et 231 al. 1999; Runge 1999; Aleman et al., 2012), Indonesia (Chabot et al., 2018) and New Guinea (Boyd 232 et al., 1998). Others researches conducted on current Central and South American plant phytoliths 233 234 complete this first overview (Piperno and Pearsall, 1998; Iriarte, 2003; Iriarte et al., 2009; Watling and Iriarte, 2013). Our phytolith classification (Table 1) is based on these regional studies and other 235 work (Iriarte, 2003; Eichhorn et al., 2010; Fenwick et al., 2011; Collura and Neumann, 2017; 236 Neumann et al., 2017), as well as the nomenclature of the ICPN working group (Madella et al., 237 2005). 238 239

240 3.3.1. Sclereid shapes (Plate I, a-c)

242	The sclereids represent a particular group associated with the sclerenchyma of woody
243	dicotyledons (Piperno, 2006) and for which the nomenclature is not well established. Many
244	morphotypes have been described in the literature; the majority exceed 50 μ m and can reach up to
245	200 µm. Some are elongated (Postek, 1981; Runge, 1999; Piperno, 2006; Garnier et al., 2013) or
246	polyhedral with a smooth, faceted surface and relatively thick edges (Kealhofer and Piperno, 1998;
247	Runge, 1999; Neumann, 2009; Garnier et al., 2013). Other morphotypes are larger, three-
248	dimensional and irregular in shape, with a smooth surface (Runge, 1999; Stromberg, 2004; Garnier
249	et al., 2013). It is also possible to find variants of this more regular morphotype in the form of large
250	smooth polyhedral with well-defined faces (Mercader et al., 2009; Garnier et al., 2013). Finally,
251	smaller, undefined shapes, between 20 and 60 μ m, may show protuberances or growths on their
252	surface (Garnier et al., 2013; Collura and Neumann, 2017). All of these morphotypes, belonging to
253	the large sclereid class, have been identified in the leaves, wood, and bark of many woody plants
254	(Runge, 1999; Piperno, 2006; Collura and Neumann, 2017).

256 3.3.2. Globular shapes (Plate I, d-k)

257

258 Spherical to ellipsoid shapes can be differentiated from their ornamentation. Globular shapes with a smooth surface have been identified many times in the tissues of woody dicotyledons 259 (Wilding and Drees, 1973; Piperno, 1988; Iriarte and Paz, 2009; Watling and Iriarte, 2013), as well 260 261 as in some monocotyledons (Runge, 1999; Bremond et al., 2004). The globular decorated shapes (warty, rough, crenellated, aggregate, etc.; Plate I, f-g) described in the literature (Piperno, 1988; 262 Alexandre et al., 1997; Kealhofer and Piperno, 1998; Barboni et al., 1999; Iriarte and Paz, 2009; 263 Garnier et al., 2013) are produced in the fruits, leaves and wood of woody dicotyledonous. 264 Sometimes the globular morphotypes are formed of aggregate particles, named globular compound 265 (Garnier et al., 2013; Collura and Neumann, 2017), or angular particles, named globular nodular 266 (Neumann et al., 2009; Collura and Neumann, 2017). In our study, all these shapes are classified 267 under the "globular mixed" category. 268

269 We chose to create a separate category for globular faceted morphotypes (Plate I, d), as they are characteristic of the Cucurbitaceae family (Piperno et al., 2000; Piperno, 2006), one of the key 270 crops of Maya societies. 271 The last globular morphotype is the globular echinate (Plate I, i-k). It is a spheroid shape 272 covered with tips. This morphotype, widely observed in the literature, is generally associated with 273 Arecaceae (Tomlinson, 1961; Piperno, 1988; Kealhofer and Piperno, 1998; Runge, 1999; Dickau et 274 al., 2013; Watling et al., 2016). However, the production of this morphotype depends on the 275 subfamily (Thomas, 2011). 276 277 3.3.3. Hat-shapes 278 279 This hat-shape morphotype (Plate I, l) is a semi-spherical shape crowned by one and several 280 thorns. It is relatively small in size: less than 25 µm (Piperno, 1988, 2006; Kealhofer and Piperno, 281 282 1998; Dickau, 2013; Iriarte and Watling., 2013; Watling et al., 2016). It is generally associated with Arecaceae but is more representative of certain subfamilies, such as Arecoideae (Thomas, 2011). 283 284 3.3.4. Grass short-cell phytolith (GSCP) shapes (Plate I, m-aa) 285 286 The grass short-cell phytoliths (GSCPs) are divided into three main morphotypes: the lobate, 287 288 saddle and rondel shapes. These three classes of phytoliths represent a great diversity of shapes and can be divided into numerous sub-variants (Mulholand, 1989; Piperno and Pearsall, 1998; Barboni 289 and Bremond, 2009; Novello et al., 2012; Neumann et al., 2017). Barboni and Bremond (2009) 290 suggest that the multiplication of sub-variants reduces the effects of taxonomic redundancy within 291 the subfamilies of Poaceae. However, other researchers claim that the development of a complex 292 classification system, with characters that are not objective and therefore difficult to reproduce from 293 one author to another, has led to an increase in the various forms and thus to errors in the 294 interpretation of assemblages (Rovner, 1971; Neumann et al., 2017). In our study, we chose to use 295

this last approach to GSCP classification to build our base (Barboni and Bremond, 2009; Neumannet al., 2017).

Lobate shapes are mainly produced by Panicoideae (Twiss, 1992; Piperno and Pearsall, 298 1998; Piperno, 2006). There are three main variants: bilobate (Plate I, m-p), cross (Plate I, q-s) and 299 polylobate (Plate I, u-v) shapes. The classification proposed by Neumann et al. (2017) classifies 300 bilobate and cross shapes according to particle size and shank length. This is particularly important 301 in our study, as it has been shown that the size of crosses could be an indicator of domesticated Zea 302 mays (Prat, 1948; Pearsall and Piperno, 1990; Iriarte, 2003). Polylobate shapes (Plate I, u-v) and 303 304 other rare shapes of lobate (e.g. triangle cross, Plate I, t) are not subdivided into variants. Saddle-shaped GSCPs are produced by Chloridoideae (Barboni and Bremond, 2009; Garnier et al., 305 2013). Because Neumann et al. (2017) point out that the different shapes of saddles can't be 306 assigned to taxonomic classification, we chose to view saddles (Plate I, w-x) as a single class of 307 GSCP. 308

The rondel morphotypes (Plate I, y-aa) show relatively large morphological variation (Mulholand, 1989; Novello et al., 2012), but are not characteristic of a Poaceae subfamily (Barboni and Bremond, 2009; Neumann et al., 2017). Thus, in our classification, rondel shapes are classified into one morphotype, except for two particular shapes (Plate I, y-z). Pearsall et al. (2003) identified a rondel shape recognizable by a top with three spaced ridges (Plate I, aa) that is both corn and teosinte specific in the Maya zone. Given the importance of maize to Maya societies, we decided to keep apart this morphotype.

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317 3.3.5. Papillae shapes (Plate I, ab-ag)

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Papillae phytolith morphotypes are associated with Cyperaceae (Ollendorf et al., 1992; Runge, 1999; Thorn, 2004; Lu et al., 2006; Honaine et al., 2009; Neumann et al., 2009; Garnier et al., 2013; Novello et al., 2018). From our observations, most papillae morphotypes have a swelling that is angular or rounded, relatively large, and generally in the center of the shape. This lump appeared hollow on all morphotypes observed. Studies have shown that, currently, it is not possible
to discuss its taxonomic assignment more precisely (Ollendorf et al., 1992; Honaine et al., 2009).
Nevertheless, each variant of papillae morphotype has been retained in our classification. The
distinctive characteristics of these variants are the general shape of the plate, its texture, the
ornamentation of the margins, and finally the size and structure of the luminous core.

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329 3.3.6. Non-diagnostic shapes and other bioindicators (Plate II)

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331 Some phytolith morphotypes are considered not diagnostic such as bulliform cells and elongate shapes. Bulliform cells are produced in the epidermis of plant leaves, from both monocots 332 and dicots (Piperno, 2006). They are rather large morphotypes, generally > 20 µm, with various 333 morphologies. In our study, we identified three bulliform shapes: cuneiform (Plate II, a-b), smooth 334 parallelepiped (Plate II, c-d) and ornamented parallelepiped (Plate II, e-f). Although they do not 335 336 have a taxonomic role, these shapes can nevertheless provide information on the ecological parameters of the deposition site, and the availability of water for certain plants in particular 337 338 (Bremond et al., 2004). The second non-diagnostic phytolith family is that of the elongate 339 morphotypes (Plate II, g-k). They are produced both in the tissues of herbaceous plants (Twiss et al., 1969; Lu and Liu, 2003) and dicotyledons (Piperno, 1988; Runge, 1999). Two subtypes can be 340 discerned: elongate smooth shapes and elongate decorated shapes. 341 342 Finally, in our non-diagnostic counts, we included sponge spicules and diatoms (Plate II, 1-

s). These non-phytoliths siliceous forms are associated with water environments and can provideinformation about wetlands.

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346 3.3.7. Use of phytolithic indices

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348 The D/P index was developed to describe the density of tree cover (Alexandre et al., 1997).
349 It is calculated as a ratio of globular shapes associated with dicotyledons to GSCPs (Alexandre et

al., 1997; Barboni et al., 1999; Bremond et al., 2004). Until now, this index has been little used in
American tropical environments (Dickau et al., 2013). In this study, we tested its effectiveness in
neotropical zones.

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354 3.4. Statistical analysis

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The statistical analysis in this study aims to attest our observations in the field, as well as the 356 results from counting the phytolith assemblages. The statistical analysis of the quadrats, which had 357 358 been grouped according to the main types of plant community, was carried out in two stages. The vegetation quadrat groupings were tested by a dissimilarity analysis using HAC (Hierarchical 359 Agglomerative Clustering) clusters. It allows verifying whether quadrat groupings in ecosystems 360 are represented by at least one similarity index, to identify poorly defined quadrats and ultimately to 361 justify our groupings in the following factor analysis. The second step in the statistical analysis of 362 363 modern vegetation environments is a component analysis. This method allowed to assign groups based on the data matrix and identify the main characteristics that contribute to this graphical 364 365 morphology: namely, plant taxa. A component analysis was performed on the quadrat/phytolith data 366 matrices. By using the plant groups identified by the HAC the scatter plot obtained by analyzing the phytoliths was compared with the analysis of the current plant communities, and at the same time, 367 the coherence between modern plant communities and phytolith assemblages was tested. 368

369

370 4. Results

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4.1 Botanical study: Plant communities at the Naachtun site

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The study of plant communities along the four transects from the *bajos* at low altitudes to the hills identified six major types of plant communities (Fig. 2 and 3). These field observations were tested by the use of a correspondence analysis.

378 4.1.1. The *Sival* zone (Plate III, f)

380	Today, almost the entire Naachtun site is covered by forest. The only exception is the Sival
381	zone, located in the northern bajo, which is characteristic of a wet savannah composed of zakaton
382	(Phragmites australis) and tul (Cyperus articulates). The wet nature of the Sival is supported by the
383	presence of lechuga (Pistia stratiotes). On the edge of the water area, an association of yerba buena
384	(Mentha x piperita) and zarza (Mimosa pigra) was observed. Wild squash, calabaza de raccoon
385	(Cucurbita radicans), was also observed at the edge of the Sival zone along transect T3. This
386	association on the edge of a Sival zone had already been observed in Naachtun's northern bajo by
387	Lundell in 1937 and was also reported by Martinez and Galindo-Leal in the Calakmul area in 2002
388	under the name <i>savana humeda</i> .
389	
390	4.1.2. The <i>Tintal</i> zone (Plate III, e)
391	
392	The Sival areas are bordered by a low forest dominated almost entirely by the tinto
393	(Haematoxylum campechianum), a small knotty tree, cracked bark, with thorny branches and small
394	leaves. These anatomical characteristics correspond to the usual adaptations of xerophytic
395	vegetation in areas with high desiccation and strong sunlight. The name of this area, <i>Tintal</i> , can be
396	explained by the predominance of this tree species. There is also a small <i>Tintal</i> zone in the southern
397	bajo (quadrat S35, transect T4, Fig. 3). This type of environment has been recorded throughout
398	northern Petén and appears characteristic of bajo areas bordering aguadas (wetland) (Lundell,
399	1937; Schulze and Whitacre, 1999; Martinez and Galindo-Leal, 2002).
400	
401	4.1.3. The <i>Chechemal</i> zone (Plate III, d)

Further away from the *Sival* zone, the concentration of *tinto* decreases and is replaced by 403 associations of shrubs belonging to the Anacardiaceae, Euphorbiaceae, Fabaceae and Myrtaceae 404 families, such as chechem negro (Metopium brownei), subin, katsin and jiesmo (Acacia sp.), 405 cascarillo (Croton sp) and guayavillo (Eugenia sp.). The Chechemal zones, being those furthest 406 from the water areas, contain some palm species, such as *cambray* (*Chamaedorea seifrizii*) and 407 escobo (Cryosophila stauracantha). The herbaceous stratum is poorly represented, with some 408 sparse zakate I (Olvra latifolia), zakate II (Kyllinga pumila), zakate III (Cyperus ochraceus) and 409 zakate de huecht (Rhynchospora cephalotes). Plant species are widely dispersed in Chechemal 410 411 environments, and their relative proportions may vary depending on the geographical area studied. Lundell (1937) does not seem to consider this plant community to be a bajo environment, but rather 412 an area of secondary regrowth. Martinez and Gallindo-Leal (2002) found the same association in 413 the Calakmul region and named it bajo mixto. Tikal, Schulze and Whitacre (1999) considered these 414 species associations to be a swamp forest environment distinct from the *Tintal* forest. We chose to 415 416 name this environment *Chechemal* due to the presence of a particular tree, the *chechem negro* (Metopium Brownei). 417

418

419 4.1.4. The *Escobal* zone (Plate III, c)

420

The northern slopes of the *bajo* and the eastern slopes of the southern *bajo* are covered by dense forest, higher than the *bajo* forests, and dominated by palm trees of the *escobo* (*Cryosophila stauracantha*) variety. Those are secondary species habitually growing in the higher areas of the site as well as *Chechemal* zones. Herbaceous plants are rare: *zakate* (*Olyra latifolia*) was observed only rarely. These dense palm forests are interpreted as the transition forests in the literature and referred to *Escobal* by Lundell (1937). They are found on the non-flooded slopes of transects T1, T3, and T4, and on the margins of the *bajo* zone along T2 (Fig. 2 and Fig. 3).

428

429 4.1.5. The *Ramonal/Zapotal* zone (Plate III, a)

431	The main vegetation on the archaeological site and hilly areas is a high forest dominated by
432	trees up to 40 meters high belonging to the Sapotaceae, Sapindaceae, Myrtacae, and Moraceae. The
433	most representative trees of this forest are the ramon (Brosimum alicastrum) and the chicozapote
434	(Manilkara zapota). It can explain why two types of high forests were identified by Lundell (1937)
435	and Schulze and Whitacre (1999): the Ramonal and Zapotal high forests. The Ramonal areas are
436	characterized by a large population of <i>ramon</i> and an undergrowth rich in populations of <i>xate</i>
437	(Chamaedorea sp.) and cordoncillo (Piper sp.). The forests of Zapotal are rich in Sapotaceae
438	species and have relatively low palm undergrowth. In 1938, Lundell proposed that the domination
439	of these resource-producing trees over the site areas should be inherited from old maintained
440	gardens. In this study, we consider these forest communities as a single forest named here
441	Ramonal/Zapotal area. In these forest environments, herbaceous plants are rare: only zakate (Olyra
442	latifolia) is occasionally found.
443	
444	4.1.6. The <i>Carrizal</i> zone (Plate III, b)
445	
446	Locally, we observed some open patches in the Ramonal/Zapotal zone (T1 and T4)
447	characterized by dense herbaceous thickets, which we refer to as Carrizal zones. Observed by
448	Lundell in Naachtun in 1937, they consist of juvenile bamboos called carrizo (Rhipidocladum
449	bartlettii). Concentrations of grass are relatively rare at the Naachtun site, meaning that the Carrizal
450	zone can be considered one of its typical plant associations. Carrizal areas do not appear to be
451	particularly associated with topographical or edaphic conditions, or archaeological structures.
452	
453	4.2. Statistical tests of plant communities
454	
455	We first used hierarchical cluster analysis to assess the validity of grouping the

hierarchy index finds initial groupings. In our case, the Euclidean hierarchy index was the most
consistent. Nonetheless, five samples (S01, S02, S16, S22, and S24) do not correspond to our initial
classification. With this HAC, S22 was interpreted as *Escobal* vegetation, while S24 was interpreted
by the analysis as *Chechemal* vegetation. The three other quadrats clearly contained transitional
vegetation and are defined as such in our statistical analysis.

462

The first two axes of the component analysis (CA) of all quadrats explain 25.0% of the total 463 variance (Fig. 5a). The contribution tables of Fig. 5 show the species that contributed most to the 464 465 morphology of the scatter plot and that are considered as ecological indicators. Axis 1 (14.6% of the 466 variance) distinguishes open habitat quadrats with Sival species, located at the positive end, from forest quadrats, located at the negative end. Axis 2 (10.4% of the variance) distinguishes plant 467 communities according to the main altitude ranges. Samples and species typical of *bajo* forests are 468 located at the positive end, while forest samples from the archaeological site, more upper, are 469 470 grouped at the negative end. Two irregularities were identified within this first CA. Quadrat S24 is interpreted to be a relatively open zone in the *bajo*, whereas it is a forest zone disturbed by a 471 compacted path at the edge of a Sival zone. This observation leads us to conclude that this sample is 472 473 problematic. The second problem is that the scatter plot corresponding to the hill vegetation environments is too condensed to discriminate the quadrats. Thus, to refine our classification, we 474 chose to perform a second CA on these samples (Fig. 5b). 475

476

For the second CA, the first three axes explain 35% of the variance. The CA conducted on the first two axes (Fig. 5b) shows that Axis 2, which explains 11.1%, is not decisive in the distribution of samples and species. Axis 1 (15.3% of the variance) distinguishes the quadrats associated with the *bajo* areas located at its negative end from the hill and site quadrats at its positive end. Axis 3 (9.4% of the variance; Fig. 5c) distinguishes the forest areas of hills with samples of the *Ramonal/Zapotal* zones at its negative end, and samples of *Carrizal* environments at its positive end 484 These conclusive statistical analyses demonstrate that our sampling and botanical survey method is 485 statistically reliable, except for the identified plant transition zones. Thus, this classification of plant 486 communities can be used to characterize modern phytolith assemblages.

487

488 4.3. Modern phytolith assemblages (Fig. 6 and Fig. 7)

489

The phytoliths counts from each quadrat have been summarized in Fig. 6 and Fig. 7. The 490 distribution diagram (Fig. 6) shows the relative abundances of phytolith morphotypes by quadrat, 491 492 grouped into plant communities. The first part of the diagram concerns the relative abundances of diagnostic morphotypes. They are expressed as a percentage of the total number of diagnostic 493 morphotypes. The second part of the diagram concerns the abundance of non-diagnostic phytoliths 494 and bioindicators. They are expressed as a percentage of the total number of counted particles. The 495 diagram of the descriptive statistics for the morphotypes (Fig. 7) shows the amplitude of the 496 497 distribution of morphotype classes across the six types of plant communities. This second diagram completes the relative abundances diagram. On these diagrams, quadrats that were not 498 discriminated by the HAC (Fig. 4; S1, S2, and S16) were not included in the calculations in Fig. 7. 499 500 Sival: Six samples are assigned to this environment (S10, S11, S12, S25, S26, and S27). The phytolith assemblages are dominated by globular mixed, GSCP (especially saddle and rondel) and 501 papillae morphotypes. On average, papillae morphotypes represent 35% of Sival assemblages, 502 503 reaching up to 85% in S10. Globular mixed, saddle and rondel phytoliths represent on average 15% of Sival assemblages but could account for over 30% (Fig. 6). The D/P index accounts 504 systematically less than 1. For bioindicators, *Sival* environments record the highest average 505 proportion of sponge spicules (30%) and diatoms (6%) of all assemblages. Analysis of the relative 506 507 abundance diagram points to differences between the assemblages in forest environments (Ramonal, Carrizal, Escobal, Chechemal, and Tintal) and wet/open environments (Sival; Fig. 6). 508 *Tintal*: Four samples are assigned to this environment (S9, S13, S28, and S35). The 509 phytolith assemblages are dominated by globular mixed, GSCP (lobate) and papillae morphotypes. 510

511 On average, globular mixed morphotypes represent 37% of *Sival* assemblages, reaching up to 50% 512 in S9 and S28 (Fig. 6 and Fig. 7). Lobate and papillae morphotypes each account for on average 513 21% of *Tintal* assemblages (Fig. 7). The D/P index oscillates between values close to 1. The 514 proportions of bioindicators are close to those observed in the *Sival*, with an average of 28% for 515 sponge spicules and 3% for diatoms.

Chechemal: Seven samples are assigned to this environment (S15, S24, S31, S32, S33, S34,
and S36). The main feature is the high percentage of globular mixed shapes, accounting for on
average 80% of assemblages but reaching up to 87% (S31 and S36; Fig. 6 and Fig. 7). Accordingly,
the D/P index values are high (15–20). As regards bioindicators, diatoms are absent, while sponge
spicules account for on average 8%.

Escobal: Eight samples are assigned to this environment (S9, S17, S18, S19, S20, S22, S23,
and S37). Globular mixed (50%) and globular echinate (40%) phytoliths are predominant (Fig. 7).
The D/P values are also very high, at 27 on average. The proportions of sponge spicules and
diatoms in these assemblages are very low (less than 1% in average).

Carrizal: Four samples are assigned to this environment (S04, S07, S41, and S42). The phytolith assemblages are dominated by globular mixed morphotypes, exceeding 60%. The most conspicuous feature is the high percentage of rondel GSCPs, accounting for 26%, and the rondel crested morphotype, reaching values around 20% (Fig. 7). The non-diagnostic phytoliths, bulliform parallelepiped and elongate psilate morphotypes are particularly well represented in these samples (Fig. 6). The D/P values are low for a forest environment, recording 3 on average. Sponge spicules and diatoms are absent.

Ramonal/Zapotal: Eight samples are assigned to this environment (S3, S5, S6, S21, S38,
S39, S40, and S43). Globular mixed and hat- shape morphotypes dominate these assemblages,
representing 65% and 18% respectively. The D/P index is extremely high, with 38 on average.
Sponge spicules and diatoms are absent.

536

537 4.4. Statistical tests of phytolith assemblages

The assembly groups defined based on the distribution diagram and ecosystems were tested 539 by a component analysis. The variables were the phytolith morphotypes and quadrat samples. The 540 contribution table of Fig. 8 indicates the morphotypes that contribute most to the morphology of the 541 scatter plot. Axis 1 and Axis 2 explain 52.7% of the variance (Fig. 8a). Axis 1, which explains 542 36.3% of the total variance, distinguishes between the openness and/or humidity of the 543 environments: the Sival and Tintal environments are located at the positive end and are mainly 544 influenced by sponge spicules, diatoms, and papillae morphotypes. GSCPs are also present at the 545 546 positive end. The negative side includes the samples taken from forest areas and morphotypes such 547 as globular mixed and globular echinate. Axis 2 of our analysis explains 16.43% of the total variance and differentiates grassy 548

undergrowth forests from forest areas with trees only. The variables on the positive side of this axis that contribute most to the morphology of the scatter plot are the rondel crested GSCP, bulliform cells and elongate morphotypes. However, the samples from *Ramonal*, *Escobal* and *Chechemal* forest areas form a group of samples that are difficult to analyze. This highlights the necessity of isolating the *Carrizal* areas from the other forest areas on the site and in the *bajo*.

554 A second CA (Fig. 8b-c) was needed to distinguish the different Naachtun forest samples (Chechemal, Ramonal/Zapotal, Escobal). The first three axes explained 73.5% of the total variance. 555 In the second graph (Fig. 8b), Axis 1 (29.2% of the variance) and Axis 2 (23.4% of the variance) 556 557 help to distinguish between the site's different forest ecosystems. The sponge spicules variable contributes considerably to the morphology of the scatter plot for these two axes, and the 558 *Chechemal* samples are therefore located in the upper right corner of the graph and isolated from 559 560 the other samples. The second contributing variable for both axes is the globular echinate morphotype, which is located on the negative part of Axis 1 and the positive part of Axis 2. This 561 562 morphotype allows to differentiate between the different Escobal-type forests (Fig. 8b). Axis 3 in the second CA suggests that hat-shape morphotypes help to distinguish between the 563 Ramonal/Zapotal samples (Fig. 8c). Finally, the vegetation samples interpreted as "undefined 564

areas" by the HAC (S1, S2, and S16; Fig. 4), were not characterized by our component analysis
either (Fig. 8).

567

568 5. Discussion

569

570 5.1. Definition and identification of Naachtun plant communities

571

The study and interpretation of phytolith assemblages show significant differences between plant formations. They point to the necessity of applying the general approach, as well as taking into account not only non-diagnostic phytoliths but also other bioindicators during the interpretation process.

The phytolith assemblages in *Sival* zones can be explained by their plant associations. Papillae morphotypes are produced by Cyperaceae, the family to which *tul* (*Cyperus articulatus*) belongs (Novello et al., 2012; Watling et al., 2013), while saddle and rondel morphotypes are produced by certain subfamilies of Poaceae, such as Arundinoideae, to which *zakaton* (*Phragmites australis*) belongs (Ollendorf et al., 1988; Piperno and Pearsall, 1998; Liu et al., 2013). The high proportions of diatoms could indicate the presence of perennial water.

582 The Tintal zones' assemblages were interpreted as assemblages of a transitional plant community between open and forest areas. The globular mixed phytoliths were most likely 583 584 produced by *tinto (Haematoxylum campechianum)*, which is the only woody dicotyledon in this plant community. The high proportions of papillae and bilobate morphotypes and other 585 bioindicators can be explained by various processes. The Sival areas contained a much higher 586 percentage of papillae morphotypes than in other studies (Barboni et al., 2007; Novello et al., 2012). 587 588 The seasonal flooding of *Sival* areas may allow for the registration of Cyperaceae tissues and 589 phytoliths, as well as diatoms and sponge spicules, in *Tintal* soils. Finally, the significant presence of bilobate morphotypes could be explained by the irregular presence of seasonal grassy 590 undergrowth, consisting of Cyperaceae and Panicoideae, as was observed in 2017. 591

592 *Chechemal* forest assemblages can be partly explained by the rare occurrences of herbaceous 593 species (Poaceae, Cyperaceae, etc.) or monocot trees, and by a predominance of the woody 594 dicotyledons that produce globular mixed morphotypes. It is principally the presence of sponge 595 spicules, due to seasonal flooding in these forest areas that permit these environments to be 596 characterized.

The palm groves of the *Escobal* environments are characterized by a predominance of both globular echinate and globular mixed which morphotypes originating from the ligneous trees of the forest. The globular echinate morphotypes are produced by certain subfamilies of Arecaceae, such as Coryphoideae (Thomas, 2015), which *escobo* (*Cryosophila stauracantha*), the dominant species in this palm grove community, belongs to. The presence of sponge spicules indicates that these areas are subjected to a seasonal flood.

The Ramonal/Zapotal high forests are defined by a phytolith association composed of 603 globular mixed and hat-shape morphotypes. Globular mixed morphotypes are produced by the 604 605 woody dicotyledons of the forest, while hat-shape morphotypes may have originated from *xate* (Chamaedorea sp.), the dominant species in this plant community. Indeed, Thomas (2015) indicates 606 607 that this morphotype is overrepresented in Arecoideae species, including the *Chamaedorea* genus. 608 However, some samples (S6, S39, S40, and S43) contained lower proportions of hat-shape morphotypes (Fig. 6). This can be explained by the fact that the Zapotal plant association, described 609 by Lundell (1937) and Schulze and Whitacre (1999), have undergrowth with lower *xate* content. 610 611 This type of assemblage could, therefore, be confused with those in the upper areas of a *bajo* that do not contain sponge spicules (S01). Within the high forest vegetation, areas with bamboo thickets 612 (*Carrizal*) were identified by an association of globular mixed, rondel crested, bulliform decorate 613 and elongate smooth morphotypes. The fact that the undergrowth is dominated by Rhipidocladum 614 *bartleddii* suggests that this bamboo species produce some of the morphotypes in this association. 615 616 The discovery of similar rondel morphotypes in other bamboos (rondel three-pikes, Pearsall et al., 2003) may confirm this hypothesis. 617

618 To conclude, three levels of interpretation of the assemblages can be highlighted. (1) The first level concerns the differentiation between forest and open areas. High proportions of GSCPs 619 and papillae shapes indicate open environments, while high proportions of globular mixed 620 morphotypes, which may or may not be accompanied by palm tree morphotypes (globular echinate 621 and hat-shape), are representative of forest environments. Forest zones with grassy undergrowth or 622 "savannahs" are characterized by high proportions of globular mixed morphotypes and one or more 623 morphotypes of GSCP or papillae, as in the case of the *Carrizal* and *Tintal* environments. (2) The 624 second level of identification concerns the wet character of the vegetation. The presence of high 625 626 proportions of papillae shapes (> 15%) in the assemblages indicates wet plant associations. As regards bioindicators, the presence of diatoms is associated with perennial water bodies, while 627 sponge spicules suggest the presence of occasional or seasonal water bodies in the *bajo* zone. This 628 is useful to identify the forest areas located in the *bajo*'s influence zone during the wet season. (3) 629 The last level of interpretation of the diagrams concerns the identification of forest areas at the 630 631 edges of hills, slopes, and *bajos*. At Naachtun, the proportion of phytoliths produced by the Arecaceae seems to be useful in distinguishing the palm transition forests and the *Ramonal* forest 632 633 from the hills of the site. 634

635 5.2. Discussion of the use of indices

636

637 5.2.1. Identify the cover layer

638

The first studies conducted using the D/P index represented the tree cover as a ratio of globular decorated, produced by woody dicotyledons, to GSCPs and morphotypes associated by some authors with Poaceae (Alexandre et al., 1997, 1999; Bremond et al., 2004, 2008). Changes in the classification of phytoliths prompted the authors to adapt this formula to the morphotypes and environments studied (Stromberg, 2004; Bremond et al., 2004; Barboni et al., 2007; Neumann et al., 644 2009; Garnier et al., 2013; Dickau et al., 2013). According to Alexandre et al. (1997), a D/P index >
645 1 is representative of open environments, while D/P values < 1 indicate forest areas.

Thus, for Naachtun plant environments, our results indicate that forest areas have high D/P 646 values recording an average of 38 for Ramonal/Zapotal samples, 27 for Escobal samples and 16 for 647 *Chechemal* samples. These values, higher than 1, are associated to dense vegetation areas, which is 648 consistent with these forest environments. In the *Sival* samples without tree strata, the D/P index 649 average was around 0.53, suggesting that the D/P index can be used to identify open environments. 650 However, *Carrizal* areas, with grassy undergrowth, and *Tintal* areas, with seasonally grassy 651 652 undergrowth, have D/P values higher than 1 but much lower than for forested areas. The average D/P index for Carrizal areas was 2.84, but varied between 1.1 and 6, while the index values for 653 Tintal zones varied between 0.36 and 2.1 (Fig. 6, Fig. 9 and Fig. 10). 654

The D/P index does not seem suitable for identifying certain plant formations whose values overlap, such as those in the *Carrizal*, *Tintal* and *Sival* zones. This is particularly true of the *Tintal* and *Sival* environments, which contain similar phytolith assemblages dominating by Cyperaceae and GSCPs. To overcome this obstacle to interpretation, we decided to adjust the D/P formula to our study by including certain useful morphotypes (Cyperaceae, sclereid, globular echinate and hatshape).

Fig. 9 shows the variation in the D/P values for each quadrat studied and compares them
with the vegetation cover values for seven different D/P index formulae. The seven formulae
correspond to a variation in the sum and type of morphotypes applied to the numerator,
denominator, or both simultaneously (Table 2).

665

The first observation leads to the conclusion that including globular echinate and hat-shape
morphotypes in the formula maximizes D/P values, especially for *Sival* zones where the D/P
average was 0.9. Thus, the use of these morphotypes in the D/P formula does not seem justified.
Including sclereid morphotypes in the index calculation does not have a significant effect on D/P
values. This can be explained by the low proportions of this morphotype in the assemblages.

671	Including papillae morphotypes in the denominator of the index significantly reduces the index
672	values for Sival (0.24 on average) and Tintal (0.98 on average) zones. If including papillae shapes
673	minimize the values for <i>Tintal</i> zones, this highlights the opening of the <i>Sival</i> zones and therefore it
674	seems necessary in our D/P index calculations. However, the simultaneous addition of sclereid
675	morphotypes to the numerator and papillae morphotypes to the denominator increases the D/P
676	values for <i>Tintal</i> zones (1.11 on average) while maintaining the best numerical representation of the
677	Sival zones (0.29 on average). Thus, for the purposes of our study, and for geographical areas where
678	papillae morphotypes make up a significant percentage of phytolith assemblages, we recommend to
679	adjust the D/P index using the following formula:
680	
681	Globular mixed + Sclereid / GSCP + Papillae
682	
683	5.2.2. Identify the mixed zones
684	
685	Even after adapting the D/P index to suit the particularities of our plant zones, it still does
686	not seem possible to use the D/P index to identify mixed zones with grassy and woody layers.
687	Indeed, our study shows that the D/P index for Carrizal and Tintal zones sometimes have the same
688	values for Sival zone. It seems, therefore, necessary to develop a new index that allows these mixed
689	zones, misinterpreted by the D/P index, to be clearly identified.
690	In this study, we propose a new index that defines a mixed zone characterized by a
691	combination of woody trees and herbaceous plants as an addition D+P. This D+P assemblage must
692	be matched with a tree D assembly and a grassy P assembly. We propose the following formula:
693	
694	[((D+P)/P + (D+P)/D)/(D+P)]x10
695	
696	which can be reduced to the form
697	
	26

698

The calculation of this formula implies that the predominance of any one part of the assembly (D or P) over the other parts will tend to minimize the denominator and thus produce high values indicating strictly forest or strictly savannah areas. Whereas a mixed assembly (D = P) will produce D/P index values of around 1, but this new index will allow the presence of both a herbaceous zone and tree stratum to be confirmed. Indeed, in such a case, the average values of D and P will increase the denominator, which will cause the index values to fall to a minimum value.

707 This new index, named LU (limits/undergrowth) index, was developed for our samples and has good potential for ecological recovery in our environmental contexts (Fig. 10). The lowest 708 values were obtained for environments containing both a herbaceous stratum and tree cover, such as 709 the Carrizal and Tintal environments. These LU values put into perspective the average D/P index 710 711 values of these environments and confirm their mixed nature. The Sival zones generated different LU index values depending on the sampling zone. The values for quadrats S12, S25 and S27 were 712 713 low and comparable to those of the Carrizal zones, which could be explained by the fact that the 714 edges of the Tintal and Ramonal zones are located nearby. Conversely, the LU index values for the samples from the center of the Sival zone (S10, S11, and S26) were higher due to the distance from 715 the wooded areas. The new index values calculated for the Escobal and Ramonal environments 716 717 were relatively high and would indicate a sparse herbaceous stratum. This is in agreement with the high D/P index values. Finally, the Chechemal environment quadrats had relatively low values 718 compared to other forest areas. Some of the low values from the new index (for quadrats \$33 and 719 S34) could correspond to forest areas where the herbaceous stratum is only seasonally present, as 720 observed in other *bajo* areas at Naachtun. Based on the quadrats and vegetation parameters (tree 721 722 cover, herbaceous undergrowth), we can define 0.25 as the maximum LU index value identifying mixed and transitional vegetation areas. 723

One main objective of this study was to test the potential of phytolith assemblages in Petén 727 728 for characterizing past landscapes and past ecosystems. The main hurdles to the development of a bioindicator tool are the different post-deposition taphonomic processes that can modify 729 thanatocoenosis and thus the interpretation of assemblages (Madella and Lancelotti, 2012). These 730 disturbance factors include the differential diagenetic recording of morphotypes (Piperno, 1988; 731 Alexandre et al., 1997), the vertical translocation of assemblages (Runge, 1999; Fishkis et al., 2010) 732 733 and lateral transport (Fredlund and Tieszen, 1994; Osterrieth et al., 2009; Madella and Lanceloti, 734 2012; Watling et al., 2016). Finally, factors making interpretation more difficult may also occur during the production and deposition of phytoliths, depending on the composition of plant 735 736 communities and sediment types.

Initially, the analysis of fossil samples, and their palaeoenvironmental interpretation must be 737 738 carried out with the awareness that "time averaging" in Holocene sediment can easily represent from several years to tens or hundreds of years (Fredlund and Tieszen, 1994; Albert et al., 2006). 739 740 For phytoliths records in fossil samples, it is difficult to know the period of the deposit. Thus, a 741 phytolith record contains a mixture of consecutive plant associations at a location over an unknown 742 number of years. However, this problem also exists for modern samples. The first centimeters of the A horizon sampled are not representative of the current vegetation, but rather of the vegetation from 743 744 a recent period which is not precisely known and could cover several months to a few decades. The part of transect T3 from the Sival zone to the southeast of the northern bajo (S24 to S27) is a good 745 example. The vegetation within the *Sival* zone is organized into specific vegetation rings linked to 746 the expansion of perennial water in spring: first the *tul/zakaton* association, then a halo of *tul* only, 747 then a *tul/verba buena/zarza* association. As observed during field missions, every spring, water 748 749 availability is different, and this affects the plant composition of quadrats S24 to S28. It can link with the spatial mobility of the *Sival* zone's plant rings depending on water precipitation. Because it 750 is a continuous phenomenon continues, 2017 samplings in the eastern Sival zone may correspond to 751

an average of phytolith records from the vegetation at different seasons. Thus, in *Sival* assemblages,
the high proportions of papillae morphotypes represent the rings of *tul* (Cyperaceae), while high
proportions of saddle shapes represent the rings of *zakaton* (Arundinoideae), and globular mixed
and sclereid morphotypes indicate the rings of *zarza* (Fabaceae).

Phytolith assemblages can be affected by lateral transport effects, caused by wind, water, 756 gravity or bioturbation (Fredlund and Tieszen, 1994; Alexandre et al., 1997; Barboni et al., 1999; 757 Piperno, 2006). The systematic approach of ecological transect sampling allows to test the 758 estimation of morphotype transport from one quadrat to another one. Alexandre et al. (1997) point 759 760 out that high tropical forests' canopies limit wind transport. However, transport by water should be 761 accounted for interpreting assemblages. At Naachtun, phytolith transport by water may be facilitated by the substantial drainage system from the high areas to the *bajo*, as well as the flooding 762 period of the *bajo* during the wet season. Our results show that phytolith assemblages are not 763 affected by transport and are most representative of the local vegetation. The vegetation of the 764 765 seasonally flooded lowlands (Sival, Tintal) is dominated by papillae polygonal and diatoms, while globular mixed morphotypes are relatively few and mainly restricted to upper woody dicot areas. 766 767 The same observation can be made for the slope area samples. The drainage of high zones does not 768 result in the mixing of phytolith associations. For example, phytolith assemblages in the transition 769 area from S7 to S8 on transect T1 are not subject to contamination from rondel crested morphotypes. Moreover, looking at the sloped area running along transect T3 (S22–S26), the upper 770 771 samples, which are rich in globular mixed morphotypes, have little influence on the D/P index value for the *bajo* samples. Thus, for the current Naachtun site, phytolith transport plays a minor role in 772 773 the alteration of phytolith assemblages.

Transport does not affect the identification of plant landscapes. However, the transport of phytoliths may play a role in the taxonomic representativeness of the quadrats studied. In all the plant communities studied, palm phytoliths were observed in an average of around 5–10% of the phytolith associations. In environments such as *Tintal* or *Sival* zones where Arecaceae are absent, these high proportions of palm phytoliths raise questions over their transport. The high numbers of

phytoliths produced by the Arecaceae and their greater resistance to erosion (Chabot et al., 2018)
could mean that they have a ubiquitous record. We surmise that comparable proportions (5–10%) of
Arecaceae phytoliths in fossil samples can be interpreted as the result of contamination caused by
transport, rather than as an identifying ecological signal.

783

784 6. Conclusion and Future Researches

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This work has allowed for the development of a tool to study paleoenvironments in the 786 787 Maya zone. Phytoliths are particularly useful in tropical forest areas where other types of fossil conservation can be lacking. The analysis of modern soil samples from Naachtun has shown the 788 potential of phytolith assemblages as bioindicators of plant landscapes in the Maya zone. A robust 789 interpretation of phytolith assemblages has been enabled both by sampling the modern soil and 790 studying the modern plant communities' distribution. We used a general approach to interpret 791 792 phytolith assemblages diagrams and multivariate statistical analyses, as well as an index approach. These results testify of the possibility to distinguish wet and open Sival areas from bajo, Tintal and 793 794 *Chechemal* forest areas. The use of both phytoliths assemblages and phytolith indices seems to be 795 particularly appropriate to differentiate opened, closed, and transitional plant environments. The 796 consistency of the results between modern plant communities and phytolith assemblages demonstrates the validity of our methodology. 797

798 However, the environments of this study are only part of Petén environments. "Natural" and "anthropic" environments were certainly much more diversified in Maya times, and are still today. 799 Thus, the realization of a current reference collection of phytoliths in anthropized areas is necessary 800 to define more precisely the interpretation of the fossil phytolith assemblages from the occupation 801 period of the Naachtun site. Some other environments, such as the savannahs of central Petén 802 (Lundell, 1937) or the drier forests of northern Yucatán could have reached the Naachtun region 803 during drier climatic periods. More humid environments of the lake or lagoon variety (Yaxha, Dos 804 Lagunas, etc.) could also have been present during wet phases. Modern soil sampling of these 805

806 environments also seems necessary to construct a complete and current phytolith reference system

807 for Maya environments on the Petén level.

Finally, the characterization of plant communities could be improved in taxonomic terms.
As we have seen, the Naachtun ecosystems are mostly dominated by woody dicotyledons. A
general study on the sclereids in such closed environments is needed to refine the taxonomic
precision. More precise taxonomy could also be achieved by combining phytolith data with the data
on other local bioindicators which are sensitive to variations in climatic parameters and ecological
plant niches.

814

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816

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- Fig. 1. Map of main archaeological sites of the Mayan lowlands and the semi-evergreen tropical
- forest location. (color)











1272 Fig. 4. HAC of plant communities in relation to quadrat species assemblages: Siv = Sival, Tin =

1273 Tintal, Che = Chechemal, Ram = Ramonal/Zapotal, Car = Carrizal, Esc = Escobal. (color)



1290 based on HAC. (color)



1298 Fig. 6. Distribution diagram of phytolith morphotypes. (color)





%

Ram

Car Esc

Tin

Siv





1310 Fig. 9. Evolution of D/P values by environments and quadrats according to the D/P index formulas

1311 used (Table 2) and vegetation cover. (color)



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Fig. 10. Evolution of the LU index as a function of the D/P index, the vegetation cover rate and the

relative frequency of a grassy undergrowth. (color)



1331	Tab.1: Classification of phytoliths encountered according to the Petén botanical families. Work to
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1334	Piperno, 2006; 8. Barboni & Bremond, 2009; 9. Honaine et al., 2009; 10. Iriarte & Paz, 2009; 11.
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1340	Bignoniaceae, Bora. = Boraginaceae, Burs. = Burseraceae, Capp. = Capparaceae, Cele. =
1341	Celestraceae, Clus. = Clusiaceae, Euph. = Euphorbiaceae, Faba. = Fabaceae, Laur. = Lauraceae,
1342	Malp. = Malpighiaceae, Malv. = Malvaceae, Melia. = Meliaceae, Mora. = Moraceae, Myrt. =
1343	Myrtaceae, Picra. = Picramniaceae, Piper. = Piperaceae, Rubi. = Rubiaceae, Sali. = Salicaceae,
1344	Sapi. = Sapindaceae, Sapo. = Sapotaceae, Cucu. = Cucurbitaceae, Lamn. = Lamniaceae); Arac. =
1345	Araceae; Arec. = Arecaceae (arec. = arecoïdeae, cory. = coryphoïdeae); Cype. = Cyperaceae; Poac.
1346	= Poaceae (bamb. = bambusoïdeae, ehrh. = ehrhartoideae, pooï. = pooïdeae, arun. = arundinoïdeae,
1347	chlo. = chloridoïdeae, pani. = panicoïdeae).
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											Tree	~							
Cod.	Morphological description	Plt.	Dicots.	Apoc. Anar.	Aral.	Bign.	Burs.	Capp.	Cele.	Clus.	Euph.	Faba.	Laur.	Malp.	Mena. Maly	Mora.	Myrt.	Picra.	Piper.
Pap.1	Plate of 1 to 3 papillae with luminous nucleus (LC)	I ab																	
Pap.2	Smooth irregular shape with short margins and a LC	I ac																	
Pap.3	Smooth irregular shape with elongated LC	I ad																	
Pap.4	Rugulate irregular hexagonal shape with LC	I ae																	
Pap.5	Rugulate irregular shape with collumelated margins with LC	I af																	
Pap.6	Smooth iiregular shape with wavy marges	I ag																	
Lob.1	3D flattened shape, with two lobes connected by a central shank	I m-p																	
Lob.2	Special form of bilobate with the outside of the hollowed lobes																		
Lob.3	3D flattened shape, with 4 lobes connected in a central point	I q-s																	
Lob.4	A special cross shape with only 3 lobes	I t																	
Lob.5	Lengthened lobate shape with at least 3 lobes	I u-v																	
Sad.		I w-x																	
Sad.1	Extended saddle shape with elongated convex sides																		
Sad.2	Saddle shape where convex sides are shorter than concave sides																		
Sad.3	Roughly parallelepiped shape with very high convex margins																		
Sad.4	Non-symmetrical saddle shape with a collapsed plane																		
Ron.																			
Ron.1	Cylindrical shape with opposite bases symmetrical or not	I y-z																	
Ron.2	Rondel shape with a head covered by ridges or thorns in 2D	I aa																	
Scl.		I a-c	4,5,7							e									
Scl.1	Elongated shape, linear or twisted, with facets		5,6			15													
Scl.2	Irregular shape covered by branches in relief		7						16		10								З
Scl.3	Irregular shape covered with pointed ornamentation		2,3,6,7				1.5									7			
Scl.4	Large irregular shape with smooth size		3,5			15										15			
Scl.5	Smooth polyhedral shape, often in parallelepiped block		4,5			15	ŝ				4	Π				15			
Glo.1	Spherical to sub-spherical shape with no visible ornamentation	Ie	2,4,5,7	15 3			3 15			13	Ξ	11,13		13		13	10		13
Glo.2	Sub-spherical shape with a rough, warty, or coarse surface	I f-g	1,2,3,4,5,6,7	13			=	~		14	2	11,13				14	. 14		13
Glo.3	Spherical to subspherical shapes grouped in the form of a complex	Ιh	5								3								
Glo.4	Big shape with an ornamented surface by large polygonal faces	Ιd					0												
Glo.5	Sub-spherical shape with a surface covered by thorns	I i-k																	
Hsh.1	Hemispherical shape covered with thorns	Π			1	1				1		1							

								6,7		2																						
	pani.							1,4,6,8,13,14,1,4,5,		1, 4, 6, 13, 14, 1, 4, 5,	8,4,5	1,7,8,13,14,5,6,7	1,4					1,4,8	13													
	chlo.							1, 4, 8, 1, 4		1,4,8,1	8		1,4,8,13,1,6,7	4,5	4,6,7,14, 4,5	14		1,4,8	13													
Herbs	arun.							1, 4, 1		4,1		1,8	1,4, 4			4		1,4,8														
	роої.							1,4		1,4		1, 4, 8	1,5					1,4,8,3,4,5	5,6	S												
	ehrh.							8	8,10,14,4,6,7				8																			
	bamb.							4,8,13,1		4,8,1		7,8	4,6	10			6,5	4, <mark>3</mark>	9													
	Poac.							3	ю	9								4,5,6,7	6,7													
	Cype.	2,5,7,9,13,16	2,6,9,13, 2		2,6,9,10,13,2,4																											
alms	cory.																														6,7,10,11	
	arec.																														3,10,13	7,13
	Arec.																														2,3,4,5,6,7	2,6,7
	Arac.																															
ş	Lamn.			_	_	_			_	_	_	_		_	_	_	_		_	_		_	_	_	_	_		_	_			
Herb	Cucu.																													7,11,2,4		
	Sapo.																										15					
rees	Sapi.																															
	Sali.																															
	Dicots.																															
	Cod.	ap.1	ap.2	c.df	ap.4	ap.5	ap.6	b.1	2b.2	b.3	b.dc	b.5	ad.	ad.1	ad.2	ad.3	ad.4	on.	n.1	3n.2	cl.	cl.1	cl.2	cl.3	cl.4	cl.5	lo.1	lo.2	lo.3	lo.4	lo.5	1
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1364	Table 2 Different	formulas	used to	calculate	the D/P	index
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	Ds:P D:Pp D:Pp Ds:Pp Dgh:P Dsgh:P Dsgh:P	Index D:P Formula (globular mixed + sclereid)/(GSCP) (globular mixed)/(GSCP) (globular mixed)/(GSCP + papillae) (globular mixed + sclereid)/(GSCP + papillae) (globular mixed + globular echinate + hat-shape)/(GSCP) (globular mixed + sclereid + globular echinate + hat-shape)/(GSCP) (globular mixed + sclereid + globular echinate + hat-shape)/(GSCP)
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1385	Tab.3 (appendix): Table of correspondence between nomens and scientific names of plant species,
1386	relative richness of nomens by plant environments: O : Dominant or typical species of an ecosystem
1387	; +++ : Species observed in at least 75% of the sampling points of an ecosystem ; ++ : Species
1388	observed in at least 50% of the sampling points of an ecosystem ; + : Species observed in at least
1389	25% of the sampling points of an ecosystem ; - : Species observed in at least one time of the
1390	sampling points of an ecosystem
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	Local name	Scientific name	Ram	Car	Esc	Che	Tin	Siv
	Amate	Ficus aurea Nutt.						
		Ficus cotinifolia Kunth				+	-	
		Ficus obtusifolia Kunth						
	Bakelac	Laetia thamnia L.	++	++	-			
	Canizte	Pouteria campechiana (Kunth) Baehni	+			-		
	Caoba	Swietenia macrophylla King				-	-	
	Catalox	Swartzia cubensis (Britton & Wilson) Standl.	-					
	Cedro	Cedrela odorata L.	-	-				
	Ceibal	Ceiba pentandra (L.) Gaertn.				-		
	Chaltecoco	Caesalpinia velutina (Britton & Rose) Standl.						
		Caesalpinia violacea (Mill.) Standl.	+	+		-		
	Chechem negro	Metopium brownei (Jacq.) Urb.				0	-	
	Chicozapote	Manilkara zapota (L.) P.Royen	0	++	++	++		
	Copal	Protium copal (Schltdl. & Cham.) Engl.	++	++	-	-		
	Guaya	Melicoccus oliviformis Kunth	++		-	-		
	Huevo de	Tabernaemontana donnell-smithii Rose ex	-			-		
	Jabin	Piscidia piscipula (L.) Sarg.	_		-	++		
	Jobillo	Astronium graveolens Jaca.	+					
	Jobo	Spondias mombin L.	++	++	+	+		
	K'olo'k	Talisia floresii Standl.	+	+	+	-		
	Limonaria	Trichilia minutiflora Standl.				-		
	Maculiz	Tabebuia heterophylla (DC.) Britton						
		Tabebuia rosea (Bertol.) Bertero ex A.DC				-		
<u>п</u> .)	Madre de Cacao	Gliricidia sepium (Jacq.) Walp.				-		
~ ~	Malerio blanco	Aspidosperma megalocarpon Müll.Arg.	+++	++	++	-		
ES ()	Manchiche	Lonchocarpus castilloi Standl.	-		-			
IRE	Mano de leon	Dendropanax arboreus (L.) Decne. & Planch.	-	-				
	Matapalo	Clusia flava Jacq.	-					
	Palo de gusano	Caesalpinia yucatanensis Greenm.						
		Lonchocarpus guatemalensis Benth.				-		
	Palo de jiote	Bursera simaruba (L.) Sarg.	+	-	-	-		
	Pimienta	Pimenta dioica (L.) Merr.	++	++	++	-		
	Ramón	Brosimum alicastrum Sw.	0	++	++	+		
	Ramón colorado	Trophis racemosa (L.) Urb.	-	-	-	-		
	Roble	Bourreria mollis Standl.				++		
		Ehretia tinifolia L.						
	Siricote	Cordia dodecandra A.DC.				-		
	Tempisque	Sideroxylon floribundum (Lundell) T.D.Penn.	-					
	Testap	Guettarda combsii Urb.	-					
	Tinto	Haematoxylum campechianum L.				++	0	
	Yasnic	Vitex gaumeri Greenm.			+	0	-	
	Zapote,	Manilkara chicle (Pittier) Gilly						
		Pouteria amygdalina (Standl.) Baehni						
		Pouteria belizensis (Standl.) Cronquist						
		Pouteria durlandii (Standl.) Baehni						
		Pouteria glomerata (Miq.) Radlk.	0	++	++	+		
		Pouteria reticulata (Engl.) Eyma						
		Pouteria viridis (Pittier) Cronquist Sideroxylon stevensonii (Standl.) Standl. &						
		Steyerm.						
		Sideroxylon tepicense (Standl.) T.D.Penn.						
SUB	Arozillo	ind.				++		
SH SH	Cacho de toro	ind.			-	+		

	Cascarillo	Croton guatemalensis Lotsy				0		
		Croton reflexifolius Kunth			-	0	-	
	Chaya	Cnidoscolus aconitifolius (Mill.) I.M.Johnst.	++	+	++	-		
	Chechem	Cameraria latifolia I			-	+		
	blanco				-	T		
	Cordoncillo	Piper amalago L.	0	++	++	-		
	_	Piper psilorhachis C.DC.						
	Guayavillo	Eugenia axillaris (Sw.) Willd.						
		Eugenia capuli (Schltdl. & Cham.) Hook. & Arn.	-			+++		
		Eugenia ibarrae Lundell						
		Eugenia tikalana Lundell						
	Jiesmo	Acacia angustissima (Mill.) Kuntze						
		Acacia dolichostachya S.F.Blake	-	-	-	++		
		Lysiloma acapulcense (Kunth) Benth.						
	Katsin	Acacia gaumeri S.F.Blake	-	-	-	+		
		Acacia riparia Kunth						
	Laurel	Nectandra coriacea (Sw.) Griseb.		_	_	_		
		Nectandra sanguinea Rol. ex Rottb.	- T	-	-	-		
	Majagua	Hampea tomentosa (C.Presl) Standl.						
		Hampea trilobata Standl.				++		
		Mortoniodendron guatemalense Standl. &						
	Manzanita	Steyerm.						
	Manzaniia	Malpighia guora L.	-	-		-		
	Mong	Maching tinatonia (L.) D.Dan av Stand						
	Mora	Maciura Incioria (L.) D.Doli ex Steud.				++	+	
	Nanze	Byrsonima buciatfolia Standi.				+		
	Palo da	Byrsonima crassifolia (L.) Kunth						
	Hormigas	Alvaradoa amorphoides Liebm.	-		-	-		
	Piñón	Jatropha curcas L.	-			-		
	Quiebrahacha	Wimmeria bartlettii Lundell						
	Subin	Wimmeria concolor Cham. & Schltdl.	-					
		Acacia collinsii Saff.						
		Acacia cornigera (L.) Willd.		-	+	+++		
	Zarza	Mimosa pigra L.						0
	Zikiya	Chrysophyllum mexicanum Brandegee						
н.		Chrysophyllum oliviforme L.			+	-		
	Bayal	Desmoncus chinantlensis Liebm. ex Mart.	-	-	+			
	Cambray	Chamaedorea seifrizii Burret	++		++	++		
	Escobo	Cryosophila stauracantha (Heynh.) R.J.Evans	++		0	+		
	Guano / Rotan	Sabal mauritiiformis (H.Karst.) Griseb. &						
MS	Guino / Doun	H.Wendl.	+	+	0	+		
PAL	Xate	Sabal mexicana Mart.						
_		Chamaedorea oblongata Mart.	0	++	+	+		
		Chamaedorea elegans Mart.						
	Bejuco de aro	Bignonia aequinoctialis L.	-					
	catabaza ae raton	Cucurbita radicans Naudin						++
	Carrizo	Rhipidocladum bartlettii (McClure) McClure		0				
	Lechuga	Pistia stratiotes L.						0
	Mozote ambra	Teucrium vesicarium Mill.						++
S	Mozote macho	Triumfetta semitriloba Jacq.						++
3RB(Navajuella	Cyperaceae ind.				-	++	+
HE	Tres marias	<i>Forchhammeria trifoliata</i> Radlk. ex Millsp.	-			-		
	Tul'	Cyperus articulatus L.						0
	Yerba buena	$Mentha \times piperita L.$						0
	Zakate ambra	Panicum trichanthum Nees					++	-
			1					

	Zakate de huecht	Rhynchospora cephalotes				+			
	Zakate I	Olyra latifolia L.	+++	++	++	++	++		
	Zakate II	Kyllinga pumila Michx.				+		+	
	Zakate III	Cyperus ochraceus Vahl				+		+	
	Zakate IV	Leptochloa virgata (L.) P.Beauv.				-	-	-	
	Zakaton	Phragmites australis (Cav.) Trin. ex Steud.						0	
	Zakaton II	Poaceae ind.						+	
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1433	Plate I Main mor	photypes of diagnostic phytoliths:	a-c: scl	ereid, o	d: gloł	oular f	aceted	, e: glo	obular
1434	psilate, f-g: globu	llar decorate, h: globular composed	l, i-k: g	lobula	r echir	nate, la	hat-sh	nape, r	n-p:

bilobate, q-s: cross, t: triangle cross, u-v: polylobate, w-x: saddle, y-z: rondel, aa: rondel crested, ab:

- 1436 papillae multiple, ac: papillae smooth, ad: papillae long, ae: papillae polygonal, af: papillae
- 1437 collumelate, ag: papillae wavy (color).



- 1440 Plate II Main morphotypes of non-diagnostic phytoliths. a-b: bulliform cuneiform, c-d: bulliform
- 1441 psilate, e-f: bulliform decorate, g-h: elongate psilate, i-k: elongate decorate, l-o: sponge spicules, p-
- 1442 s: diatoms. (color)



1452 d: Chechemal, e: Tintal, f: Sival. (color)

