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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 phytolith 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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20

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

28 Abstract

29

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

45

46 Keywords

47

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

49

50 1. Introduction

51

52 Today, while more and more studies are focusing on the systemic collapse of our modern
53 civilization (Meadows et al., 2004; Erhlich and Ehrlich, 2013; Servigne and Stevens, 2015), some
54 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,
56 well known for their huge architectural remains, are a good example. Studies testify to two major
57 collapse events that occurred in the 2nd century (pre-classical collapse) and the 10th century
58 (classical collapse) CE. While these collapse events are sometimes presented as the result of overly
59 intensive environmental exploitation (Abrams and Rue, 1988; Hansen et al. 2002; Lentz and
60 Hockaday, 2009; Turner and Sabloff, 2012), other authors question this hypothesis by citing the
61 Maya's considered and sustainable management of forest and plant resources (Fedick, 2010;
62 Mcneil, 2012; Lentz et al., 2015; Thompson et al., 2015).

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

77 In order to understand the link between past cultural and environmental changes, this study
78 uses both the archaeological context and geomorphological/palaeoenvironmental context. Naachtun
79 is located on a large hilly escarp and is bordered to the north and south by two depressions of the
80 karstic polje type (Castanet et al. 2016), called *bajos*, with dispersed perennial wetlands, locally
81 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.

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

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

107 The aim of this study is, therefore, to assess the potential of phytoliths in the Maya
108 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
110 ecosystems of the Naachtun site. For each quadrat, surface soils were sampled and phytolith
111 assemblages analyzed using the general counting and index approaches. The link between phytolith
112 assemblages and plant communities was tested using a distribution diagram, and also a statistical
113 study using a component analysis. In this paper, we will compare the different phytolith indexes and
114 propose a new index to better establish the landscape characteristics of these communities.

115

116 2. Study Area

117

118 2.1. Climate and geology

119

120 The department of Petén is located in the southern part of the Petén tropical forest covering
121 the central lowlands of the Yucatán peninsula, also referred as the Maya Lowlands (Fig. 1). The
122 vegetation of Petén is mainly subject to two control factors: precipitations and regional
123 geomorphology (Sánchez-Sánchez and Islebe, 2002; Carrillo-Bastos et al., 2012). Indeed, seasonal
124 latitudinal migrations of the Inter-Tropical Convergence Zone (ITCZ) and the North Atlantic High
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
127 1,500 mm, is concentrated in the period from May to December, while the period from January to
128 April corresponds to a dry season. Due to the intertropical position of the peninsula, temperatures
129 remain relatively stable throughout the year (Wilson, 1980). These umbrothermal conditions
130 correspond to an Am-type climate in the Köppen classification (Pennington and Sarukhán, 2005).
131 The regional geomorphology of Petén is a vast Meso-Cenozoic carbonate platform, composed
132 mainly of limestone, at low altitude (250–300 m). The fractures and heterogeneities of the limestone
133 bedrock have produced karstified landscapes resulting in hills alternating with depressions (*bajos*)
134 (Dunning et al., 2002; Beach et al., 2008, 2009). Consequently, differences in hydrology and soil

135 composition are also observed, with thin layers of well-drained rendosol on hill and slope areas, and
136 seasonally waterlogged vertisol-histosol in *bajo* areas (Beach et al., 2008).

137

138 2.2. The plant formations of Petén

139

140 The Petén forest was first described in the 1930s by Lundell (1937) and was defined as a
141 semi-sempervirent tropical forest. However, this ecological classification does not reflect the true
142 diversity of forest ecosystems found in the different geomorphological contexts of Petén. The hill
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,
145 Moraceae, Sapindaceae, and Sapotaceae. The relatively sparse undergrowth is occupied by
146 Arecaceae and Piperaceae shrubs, and a small number of grassy plants. The *bajo* areas are covered
147 by a low forest (5–8 m), where plant associations are adapted to clayey soils and the seasonal
148 submersions and drying periods. These are mainly composed of species belonging to the
149 Anacardiaceae, Euphorbiaceae, Fabaceae and Myrtaceae families. The *bajo* forest undergrowth is
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;
153 Schulze and Whitacre, 1999). Currently, the Petén forests are less populated than during the Maya
154 period (Canuto et al., 2018).

155

156 3. Methodology

157

158 3.1. Vegetation study and soil sampling

159

160 The vegetation study was conducted during two fieldwork sessions at the end of the dry
161 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
163 (T1, T2, and T3), and one north-south/west oriented transect (T4), over distances of about one
164 kilometer. These transects therefore covered different plant formations of forests and herbaceous
165 areas from hills and *bajo* (Fig. 2). Along these transects, we identified areas where plant
166 communities were changing. Depending on the extent of a plant community, one to two blocks,
167 each of about 100m², have been positioned in the middle of it. On each quadrat, we recorded the
168 plant species presences based on local common names and annotated their relative quantity.
169 Vegetation cover values were estimated from colorimetric processing (light rate [light-white pixels]
170 relative to vegetation coverage rate [dark pixels]) of forest cover photographs taken vertically and to
171 up. Finally, for the phytolith analysis, only a few grams of the surface portion of the A1 horizon
172 (the A0 litter having been removed from the sample) were taken from several locations in each of
173 the quadrat. All samples were mixed to create a single sample of approximately 100 g by quadrat. It
174 allowed us to prevent our sampling producing ultra-local biases in phytolith assemblages.

175

176 The ecological survey was carried out with the help of a local forester able to identify the
177 plants by their vernacular names in Spanish and/or Mayan. The vernacular names were then
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.,
180 2004), while some plant specimens were compared with taxonomic types from the Paris Herbarium
181 in France's National Museum of Natural History (MNHN). However, the local nomenclature of
182 Naachtun plants contains many synonymies (one local name = different taxa) or polynomials
183 (several local names = one taxon). To resolve this issue, we chose to apply taxonomic corrections,
184 such as the following:

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

188 - Construction of species complex: *Manilkara chicle*, *Pouteria glomerata*, *Pouteria*
189 *reticulata*, *Sideroxylon tepicense*, trees belonging to the Sapotaceae family, are all named *zapote* or
190 *zapotillo*. In such cases, we decided to group all these scientific names under the nomen *zapote*.
191 Phytoliths do not allow for differentiation between woody dicotyledon species. We, therefore, chose
192 to create species complexes for trees (62 nomens associated with woody dicotyledons). Phytoliths
193 are, however, a good tool for characterizing monocotyledon families, such as Arecaceae,
194 Cyperaceae, Commelinaceae, Musaceae, and Poaceae (Piperno, 2006; Honaine et al., 2009;
195 Eichhorn et al., 2010; Novello et al., 2012; Chen and Smith, 2013). With some families, it is
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
198 the 157 initial occurrences, 75 nomens were assigned to a genus and five nomens to a family (See
199 Table 3 in appendix). It should be noted that these sampling and identification methods were
200 designed to be used primarily on ecological rather than taxonomic assemblages.

201 Plant associations were studied by quadrat using a statistical study of nomen occurrences.
202 Each nomen class selected was classified for each of the quadrats based on the following criteria:
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
205 classification coupled with a factor analysis of the correspondences. This statistical methodology
206 aimed to verify the representativeness of the assemblages across the site and compare them with the
207 literature (Lundell, 1937; Schulze and Whitacre, 1999; Martínez and Galindo-Leal, 2002).

208

209 3.2. Preparation and counting of phytolithes

210

211 The procedure for phytolith extraction was adapted from Piperno (2006). For approximately
212 20 g of soil: (1) Organic Matter was destroyed using hydrogen peroxide (H₂O₂), (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.

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

226

227 3.3. Classification of phytolithes

228

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

239

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

241

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 μm 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 μm , 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).

255

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

257

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

269 We chose to create a separate category for globular faceted morphotypes (Plate I, d), as they
270 are characteristic of the Cucurbitaceae family (Piperno et al., 2000; Piperno, 2006), one of the key
271 crops of Maya societies.

272 The last globular morphotype is the globular echinate (Plate I, i-k). It is a spheroid shape
273 covered with tips. This morphotype, widely observed in the literature, is generally associated with
274 Arecaceae (Tomlinson, 1961; Piperno, 1988; Kealhofer and Piperno, 1998; Runge, 1999; Dickau et
275 al., 2013; Watling et al., 2016). However, the production of this morphotype depends on the
276 subfamily (Thomas, 2011).

277

278 3.3.3. Hat-shapes

279

280 This hat-shape morphotype (Plate I, l) is a semi-spherical shape crowned by one and several
281 thorns. It is relatively small in size: less than 25 μm (Piperno, 1988, 2006; Kealhofer and Piperno,
282 1998; Dickau, 2013; Iriarte and Watling., 2013; Watling et al., 2016). It is generally associated with
283 Arecaceae but is more representative of certain subfamilies, such as Arecoideae (Thomas, 2011).

284

285 3.3.4. Grass short-cell phytolith (GSCP) shapes (Plate I, m-aa)

286

287 The grass short-cell phytoliths (GSCPs) are divided into three main morphotypes: the lobate,
288 saddle and rondel shapes. These three classes of phytoliths represent a great diversity of shapes and
289 can be divided into numerous sub-variants (Mulholland, 1989; Piperno and Pearsall, 1998; Barboni
290 and Bremond, 2009; Novello et al., 2012; Neumann et al., 2017). Barboni and Bremond (2009)
291 suggest that the multiplication of sub-variants reduces the effects of taxonomic redundancy within
292 the subfamilies of Poaceae. However, other researchers claim that the development of a complex
293 classification system, with characters that are not objective and therefore difficult to reproduce from
294 one author to another, has led to an increase in the various forms and thus to errors in the
295 interpretation of assemblages (Rovner, 1971; Neumann et al., 2017). In our study, we chose to use

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

298 Lobate shapes are mainly produced by Panicoideae (Twiss, 1992; Piperno and Pearsall,
299 1998; Piperno, 2006). There are three main variants: bilobate (Plate I, m-p), cross (Plate I, q-s) and
300 polylobate (Plate I, u-v) shapes. The classification proposed by Neumann et al. (2017) classifies
301 bilobate and cross shapes according to particle size and shank length. This is particularly important
302 in our study, as it has been shown that the size of crosses could be an indicator of domesticated Zea
303 mays (Prat, 1948; Pearsall and Piperno, 1990; Iriarte, 2003). Polylobate shapes (Plate I, u-v) and
304 other rare shapes of lobate (e.g. triangle cross, Plate I, t) are not subdivided into variants.

305 Saddle-shaped GSCPs are produced by Chloridoideae (Barboni and Bremond, 2009; Garnier et al.,
306 2013). Because Neumann et al. (2017) point out that the different shapes of saddles can't be
307 assigned to taxonomic classification, we chose to view saddles (Plate I, w-x) as a single class of
308 GSCP.

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

316

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

318

319 Papillae phytolith morphotypes are associated with Cyperaceae (Ollendorf et al., 1992;
320 Runge, 1999; Thorn, 2004; Lu et al., 2006; Honaine et al., 2009; Neumann et al., 2009; Garnier et
321 al., 2013; Novello et al., 2018). From our observations, most papillae morphotypes have a swelling
322 that is angular or rounded, relatively large, and generally in the center of the shape. This lump

323 appeared hollow on all morphotypes observed. Studies have shown that, currently, it is not possible
324 to discuss its taxonomic assignment more precisely (Ollendorf et al., 1992; Honaine et al., 2009).
325 Nevertheless, each variant of papillae morphotype has been retained in our classification. The
326 distinctive characteristics of these variants are the general shape of the plate, its texture, the
327 ornamentation of the margins, and finally the size and structure of the luminous core.

328

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

330

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

342 Finally, in our non-diagnostic counts, we included sponge spicules and diatoms (Plate II, l-
343 s). These non-phytoliths siliceous forms are associated with water environments and can provide
344 information about wetlands.

345

346 3.3.7. Use of phytolithic indices

347

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

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

353

354 3.4. Statistical analysis

355

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

369

370 4. Results

371

372 4.1 Botanical study: Plant communities at the Naachtun site

373

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

377

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

379

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 articulatus*). 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 *savana humeda*.

389

390 4.1.2. The *Tintal* 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, *Tintal*, can be
396 explained by the predominance of this tree species. There is also a small *Tintal* 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 *Chechemal* zone (Plate III, d)

402

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

418

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

420

421 The northern slopes of the *bajo* and the eastern slopes of the southern *bajo* are covered by
422 dense forest, higher than the *bajo* forests, and dominated by palm trees of the *escobo* (*Cryosophila*
423 *stauracantha*) variety. Those are secondary species habitually growing in the higher areas of the site
424 as well as *Chechemal* zones. Herbaceous plants are rare: *zakate* (*Olyra latifolia*) was observed only
425 rarely. These dense palm forests are interpreted as the transition forests in the literature and referred
426 to *Escobal* by Lundell (1937). They are found on the non-flooded slopes of transects T1, T3, and
427 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)

430

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, Myrtaceae, 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 *ramon* and an undergrowth rich in populations of *xate*
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 *Carrizal* 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
456 environments into six ecosystems (Fig. 4). The HAC checks, in the form of a cluster, whether a

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

462

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

476

477 For the second CA, the first three axes explain 35% of the variance. The CA conducted on
478 the first two axes (Fig. 5b) shows that Axis 2, which explains 11.1%, is not decisive in the
479 distribution of samples and species. Axis 1 (15.3% of the variance) distinguishes the quadrats
480 associated with the *bajo* areas located at its negative end from the hill and site quadrats at its
481 positive end. Axis 3 (9.4% of the variance; Fig. 5c) distinguishes the forest areas of hills with
482 samples of the *Ramonal/Zapotal* zones at its negative end, and samples of *Carrizal* environments at
483 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

490 The phytoliths counts from each quadrat have been summarized in Fig. 6 and Fig. 7. The
491 distribution diagram (Fig. 6) shows the relative abundances of phytolith morphotypes by quadrat,
492 grouped into plant communities. The first part of the diagram concerns the relative abundances of
493 diagnostic morphotypes. They are expressed as a percentage of the total number of diagnostic
494 morphotypes. The second part of the diagram concerns the abundance of non-diagnostic phytoliths
495 and bioindicators. They are expressed as a percentage of the total number of counted particles. The
496 diagram of the descriptive statistics for the morphotypes (Fig. 7) shows the amplitude of the
497 distribution of morphotype classes across the six types of plant communities. This second diagram
498 completes the relative abundances diagram. On these diagrams, quadrats that were not
499 discriminated by the HAC (Fig. 4; S1, S2, and S16) were not included in the calculations in Fig. 7.

500 *Sival*: Six samples are assigned to this environment (S10, S11, S12, S25, S26, and S27). The
501 phytolith assemblages are dominated by globular mixed, GSCP (especially saddle and rondel) and
502 papillae morphotypes. On average, papillae morphotypes represent 35% of *Sival* assemblages,
503 reaching up to 85% in S10. Globular mixed, saddle and rondel phytoliths represent on average 15%
504 of *Sival* assemblages but could account for over 30% (Fig. 6). The D/P index accounts
505 systematically less than 1. For bioindicators, *Sival* environments record the highest average
506 proportion of sponge spicules (30%) and diatoms (6%) of all assemblages. Analysis of the relative
507 abundance diagram points to differences between the assemblages in forest environments
508 (*Ramonal*, *Carrizal*, *Escobal*, *Chechemal*, and *Tintal*) and wet/open environments (*Sival*; Fig. 6).

509 *Tintal*: Four samples are assigned to this environment (S9, S13, S28, and S35). The
510 phytolith assemblages are dominated by globular mixed, GSCP (lobate) and papillae morphotypes.

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.

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

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

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

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

536

537 4.4. Statistical tests of phytolith assemblages

538

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

548 Axis 2 of our analysis explains 16.43% of the total variance and differentiates grassy
549 undergrowth forests from forest areas with trees only. The variables on the positive side of this axis
550 that contribute most to the morphology of the scatter plot are the rondel crested GSCP, bulliform
551 cells and elongate morphotypes. However, the samples from *Ramonal*, *Escobal* and *Chechemal*
552 forest areas form a group of samples that are difficult to analyze. This highlights the necessity of
553 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
555 (*Chechemal*, *Ramonal/Zapotal*, *Escobal*). The first three axes explained 73.5% of the total variance.
556 In the second graph (Fig. 8b), Axis 1 (29.2% of the variance) and Axis 2 (23.4% of the variance)
557 help to distinguish between the site's different forest ecosystems. The sponge spicules variable
558 contributes considerably to the morphology of the scatter plot for these two axes, and the
559 *Chechemal* samples are therefore located in the upper right corner of the graph and isolated from
560 the other samples. The second contributing variable for both axes is the globular echinate
561 morphotype, which is located on the negative part of Axis 1 and the positive part of Axis 2. This
562 morphotype allows to differentiate between the different *Escobal*-type forests (Fig. 8b). Axis 3 in
563 the second CA suggests that hat-shape morphotypes help to distinguish between the
564 *Ramonal/Zapotal* samples (Fig. 8c). Finally, the vegetation samples interpreted as "undefined

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

567

568 5. Discussion

569

570 5.1. Definition and identification of Naachtun plant communities

571

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

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

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

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.

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

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

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

639 The first studies conducted using the D/P index represented the tree cover as a ratio of
640 globular decorated, produced by woody dicotyledons, to GSCPs and morphotypes associated by
641 some authors with *Poaceae* (Alexandre et al., 1997, 1999; Bremond et al., 2004, 2008). Changes in
642 the classification of phytoliths prompted the authors to adapt this formula to the morphotypes and
643 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.

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

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

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

665

666 The first observation leads to the conclusion that including globular echinate and hat-shape
667 morphotypes in the formula maximizes D/P values, especially for *Sival* zones where the D/P
668 average was 0.9. Thus, the use of these morphotypes in the D/P formula does not seem justified.
669 Including sclereid morphotypes in the index calculation does not have a significant effect on D/P
670 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 *Tintal* zones, this highlights the opening of the *Sival* 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 *Tintal* 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
$$[((D+P)/P + (D+P)/D)/(D+P)] \times 10$$

695

696 which can be reduced to the form

697

698 $[(D+P)/(D*P)]x10$

699

700 The calculation of this formula implies that the predominance of any one part of the
701 assembly (D or P) over the other parts will tend to minimize the denominator and thus produce high
702 values indicating strictly forest or strictly savannah areas. Whereas a mixed assembly (D = P) will
703 produce D/P index values of around 1, but this new index will allow the presence of both a
704 herbaceous zone and tree stratum to be confirmed. Indeed, in such a case, the average values of D
705 and P will increase the denominator, which will cause the index values to fall to a minimum value.
706

707 This new index, named LU (limits/undergrowth) index, was developed for our samples and
708 has good potential for ecological recovery in our environmental contexts (Fig. 10). The lowest
709 values were obtained for environments containing both a herbaceous stratum and tree cover, such as
710 the *Carrizal* and *Tintal* environments. These LU values put into perspective the average D/P index
711 values of these environments and confirm their mixed nature. The *Sival* zones generated different
712 LU index values depending on the sampling zone. The values for quadrats S12, S25 and S27 were
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
715 samples from the center of the *Sival* zone (S10, S11, and S26) were higher due to the distance from
716 the wooded areas. The new index values calculated for the *Escobal* and *Ramonal* environments
717 were relatively high and would indicate a sparse herbaceous stratum. This is in agreement with the
718 high D/P index values. Finally, the *Chechemal* environment quadrats had relatively low values
719 compared to other forest areas. Some of the low values from the new index (for quadrats S33 and
720 S34) could correspond to forest areas where the herbaceous stratum is only seasonally present, as
721 observed in other *bajo* areas at Naachtun. Based on the quadrats and vegetation parameters (tree
722 cover, herbaceous undergrowth), we can define 0.25 as the maximum LU index value identifying
723 mixed and transitional vegetation areas.

724

725 5.3. Development of a paleoenvironmental tool for Maya archaeology

726

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

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

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

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

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

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

783

784 6. Conclusion and Future Researches

785

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

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

806 environments also seems necessary to construct a complete and current phytolith reference system
807 for Maya environments on the Petén level.

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

814

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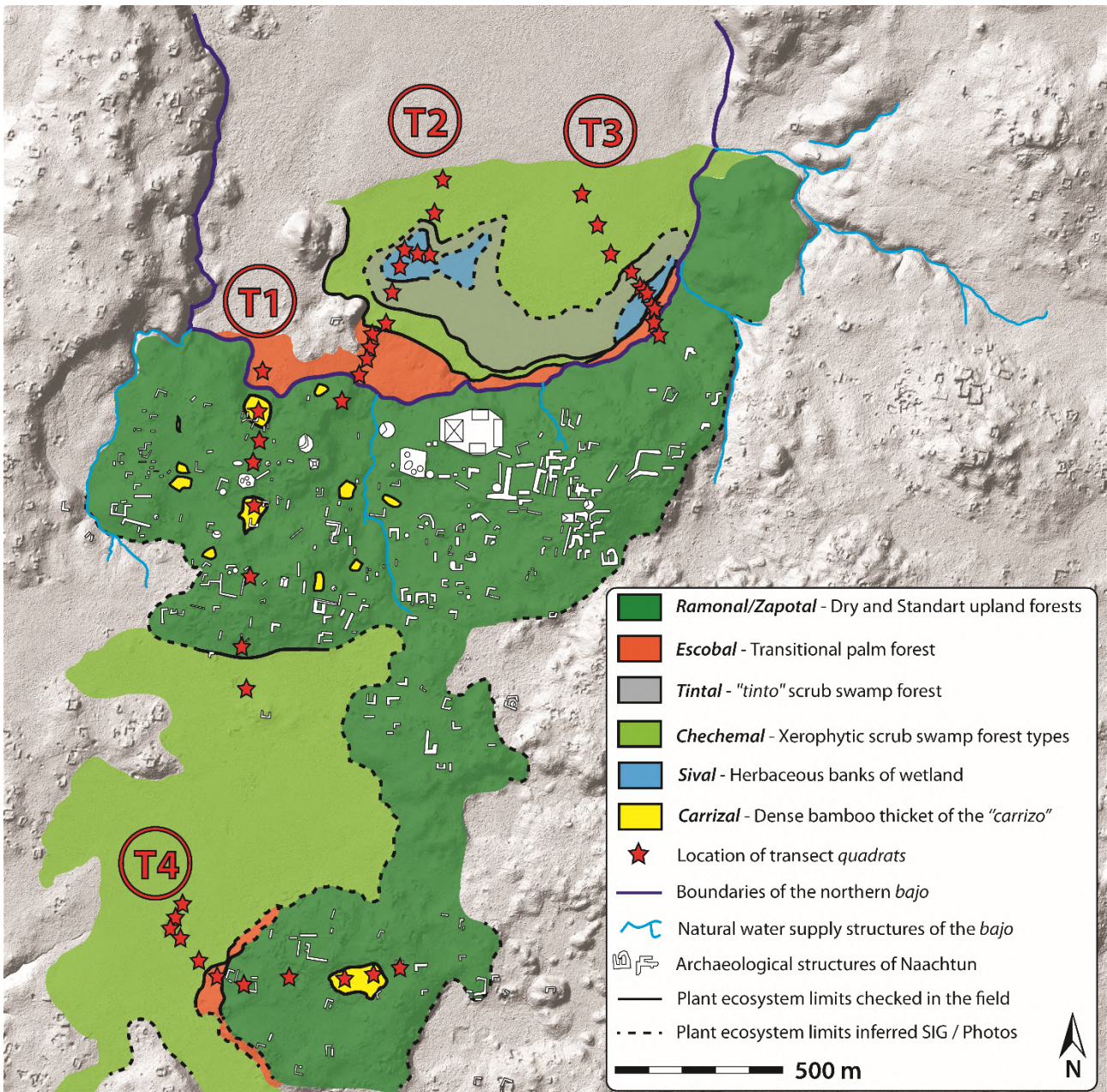
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1254 Fig. 1. Map of main archaeological sites of the Mayan lowlands and the semi-evergreen tropical
1255 forest location. (color)
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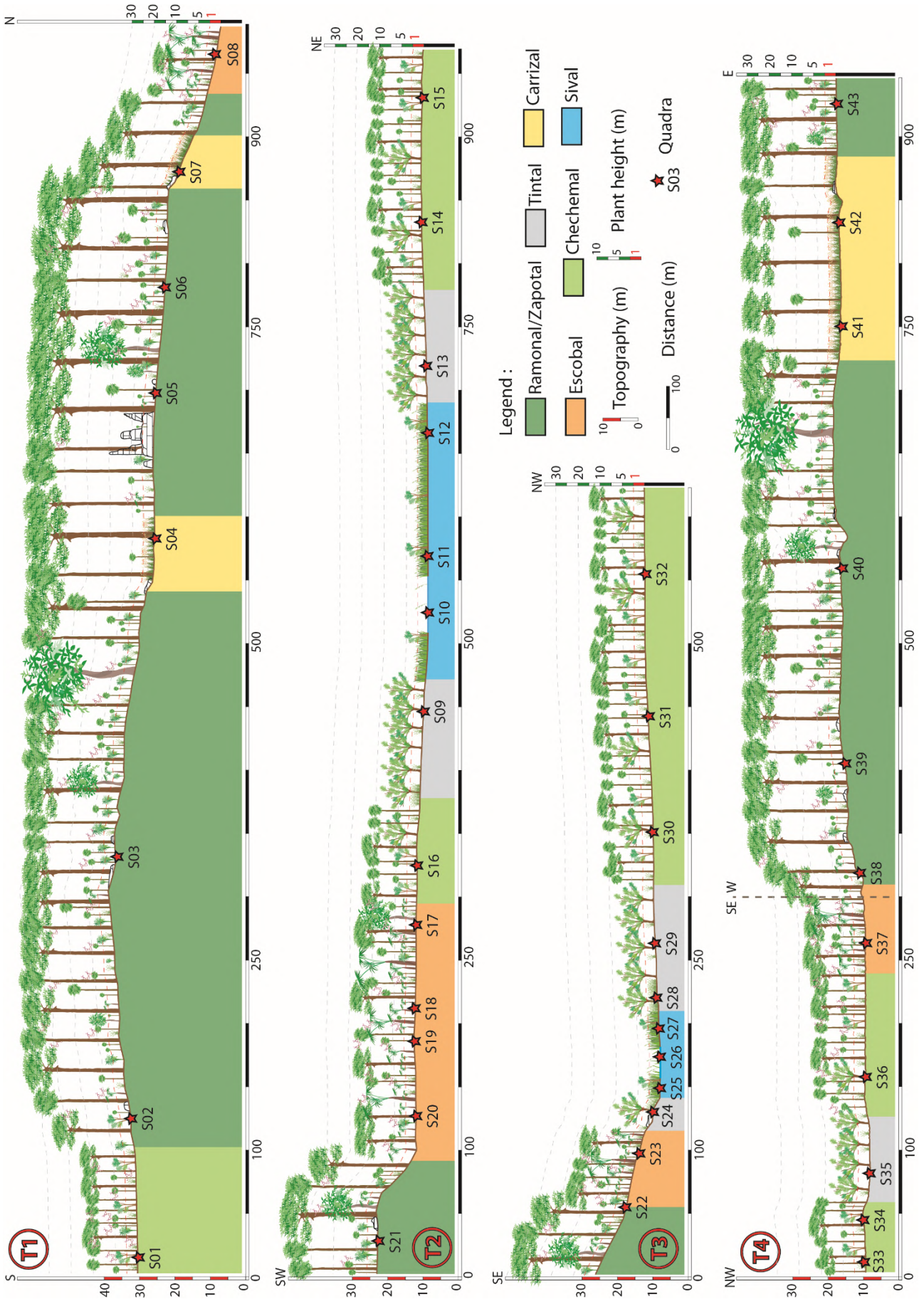


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1260 Fig. 2. Map of plant communities and ecological quadrats location. (color)

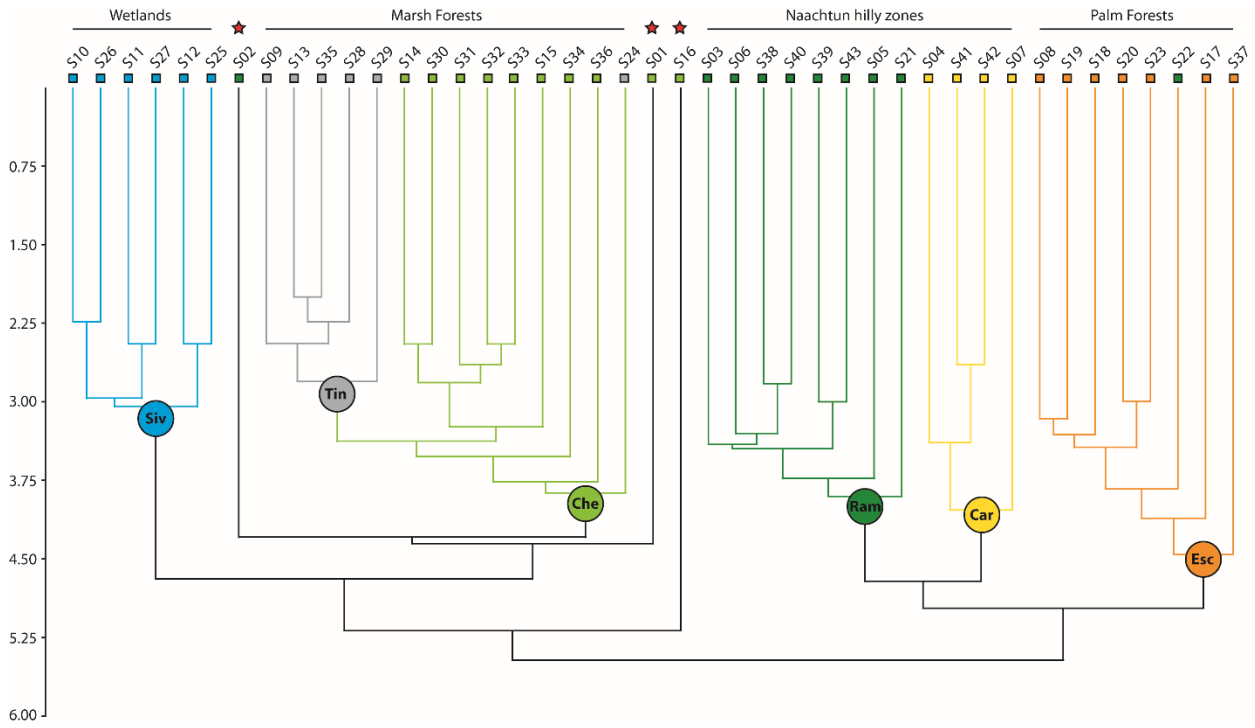


1270 Fig. 3. Ecological transects with plant communities, elevations and quadrat locations. (color)



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1272 Fig. 4. HAC of plant communities in relation to quadrat species assemblages: Siv = Sival, Tin =
 1273 Tintal, Che = Chechemical, Ram = Ramonal/Zapotal, Car = Carrizal, Esc = Escobal. (color)



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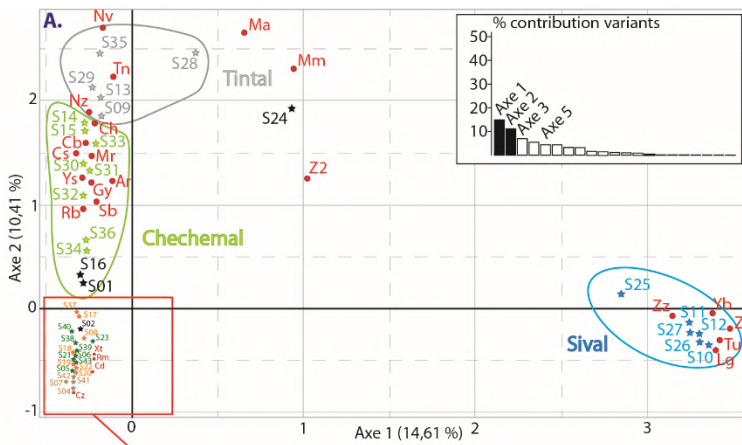
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1289 Fig. 5. CA relating to data on the presence of plant species; the plant communities are selected
 1290 based on HAC. (color)

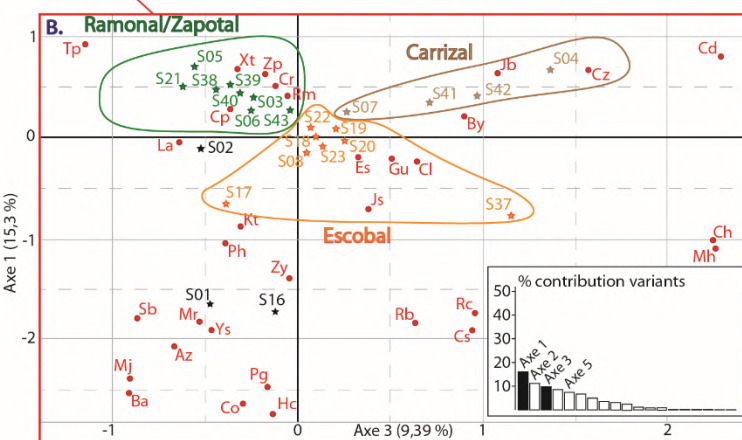


Axe 1

Variab.	Vb.	Cord.	Ctrb.
Zarza	Zz	3,11	24,6 %
Yerba bn.	Yb	3,28	21,1 %
Zakaton	Zk	3,37	17,8 %
Tul	Tu	3,39	13,5 %
Lechuga	Lg	3,41	4,5 %
Arozillo	Az	3,13	3,8 %

Axe 2

Variab.	Vb.	Cord.	Ctrb.
Tinto	Tn	2,18	23,5 %
Chechem N.	Ch	1,78	6,9 %
Cascarillo	Cs	1,37	5,1 %
Navajuel	Nv	2,70	4,0 %
Mozote A.	Ma	2,66	3,9 %
Guayavillo	Gy	1,26	3,5 %
Arozillo	Az	1,25	3,4 %
Yasnic	Ys	1,31	3,3 %
Nanze	Nz	1,83	2,7 %
Mora	Mr	1,39	2,7 %
Roble	Rb	1,09	2,3 %
Caoba	Co	1,50	1,8 %
Zakate II	Zz	1,26	1,7 %
Mozote M.	Mm	2,32	1,5 %
Subin	Sb	1,12	1,4 %
Carrizo	Cz	-0,80	-1,4 %
Cordoncil.	Cr	-0,59	-2,9 %
Ramon	Rm	-0,61	-2,8 %
Xate	Xt	-0,55	-1,7 %

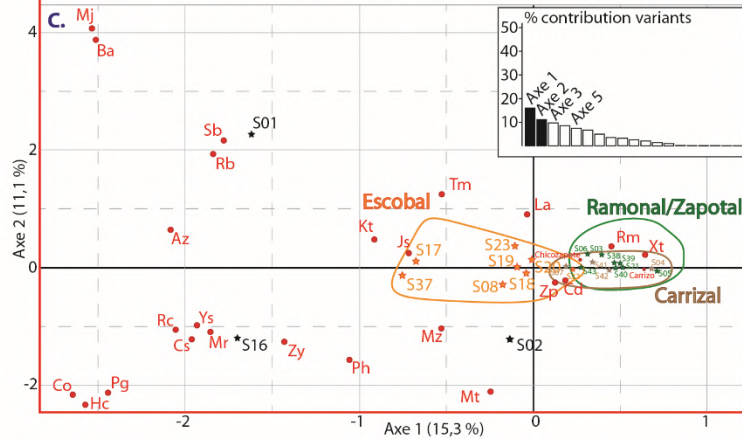


Axe 1

Variab.	Vb.	Cord.	Ctrb.
Xate	Xt	0,62	4,8 %
Ramon	Rm	0,46	3,7 %
Cordoncil.	Cr	0,38	2,7 %
Carrizo	Cz	0,63	2,0 %
Chicozap.	Cp	0,42	2,0 %
Zapote	Zp	0,37	1,8 %
Palo Horm.	Ph	-0,99	-1,9 %
Zikiya	Zy	-1,40	-2,8 %
Jiesmo	Js	-0,70	-2,5 %
Katsin	Kt	-0,90	-3,0 %
Subin	Sb	-1,78	-4,0 %
Bejuco aro	Ba	-2,53	-4,0 %
Majagua	Mj	-2,53	-4,0 %
Mora	Mr	-1,84	-4,3 %
Caoba	Co	-2,64	-4,4 %
Huev Cab.	Hc	-2,64	-4,4 %
Palo Gus.	Pg	-2,64	-4,4 %
Cascarillo	Cs	-1,90	-4,5 %
Ramon Col.	Rc	-1,90	-4,5 %
Arozillo	Az	-2,07	-8,0 %

Axe 2

Variab.	Vb.	Cord.	Ctrb.
Carrizo	Cz	1,57	19,8 %
Cedro	Cd	2,27	10,4 %
Bayal	By	0,87	5,4 %
Chechem N.	Ch	2,24	5,1 %
Manchiche	Mh	2,24	5,1 %
Guano	Gn	0,50	4,5 %
Copal	Cl	0,61	4,1 %
Jobillo	Jb	1,09	3,6 %
Cascarillo	Cs	0,99	2,0 %
Ramon Col.	Rc	0,99	2,0 %
Escobo	Es	0,29	1,9 %
Cordoncil.	Cr	-0,24	-1,8 %
Xate	Xt	-0,35	-2,5 %
Laurel	La	-0,65	-2,5 %
Tempisq.	Tp	-1,13	-2,6 %



Axe 1

Variab.	Vb.	Cord.	Ctrb.
Xate	Xt	0,62	4,8 %
Ramon	Rm	0,46	3,7 %
Cordoncil.	Cr	0,38	2,7 %
Carrizo	Cz	0,63	2,0 %
Chicozap.	Cp	0,42	2,0 %
Zapote	Zp	0,37	1,8 %
Palo Horm.	Ph	-0,99	-1,9 %
Zikiya	Zy	-1,40	-2,8 %
Jiesmo	Js	-0,70	-2,5 %
Katsin	Kt	-0,90	-3,0 %
Subin	Sb	-1,78	-4,0 %
Bejuco aro	Ba	-2,53	-4,0 %
Majagua	Mj	-2,53	-4,0 %
Mora	Mr	-1,84	-4,3 %
Caoba	Co	-2,64	-4,4 %
Huev Cab.	Hc	-2,64	-4,4 %
Palo Gus.	Pg	-2,64	-4,4 %
Cascarillo	Cs	-1,90	-4,5 %
Ramon Col.	Rc	-1,90	-4,5 %
Arozillo	Az	-2,07	-8,0 %

Axe 2

Variab.	Vb.	Cord.	Ctrb.
Bejuca aro	Ba	4,14	14,8 %
Majagua	Mj	4,14	14,8 %
Subin	Sb	2,15	8,0 %
Roble	Rb	1,95	6,6 %
Tres marias	Tm	1,28	5,6 %
Laurel	La	0,74	2,8 %
Cascarillo	Cs	-1,20	-2,5 %
Ramon Col.	Rc	-1,20	-2,5 %
Zikiya	Zy	-1,30	-2,9 %
Manzanita	Mz	-0,99	-3,4 %
Matapalo	Mt	-2,04	-3,6 %
Caoba	Co	-2,15	-4,0 %
Huevo Cab.	Hc	-2,15	-4,0 %
Palo Gus.	Pg	-2,15	-4,0 %
Palo Horm.	Ph	-1,55	-6,2 %

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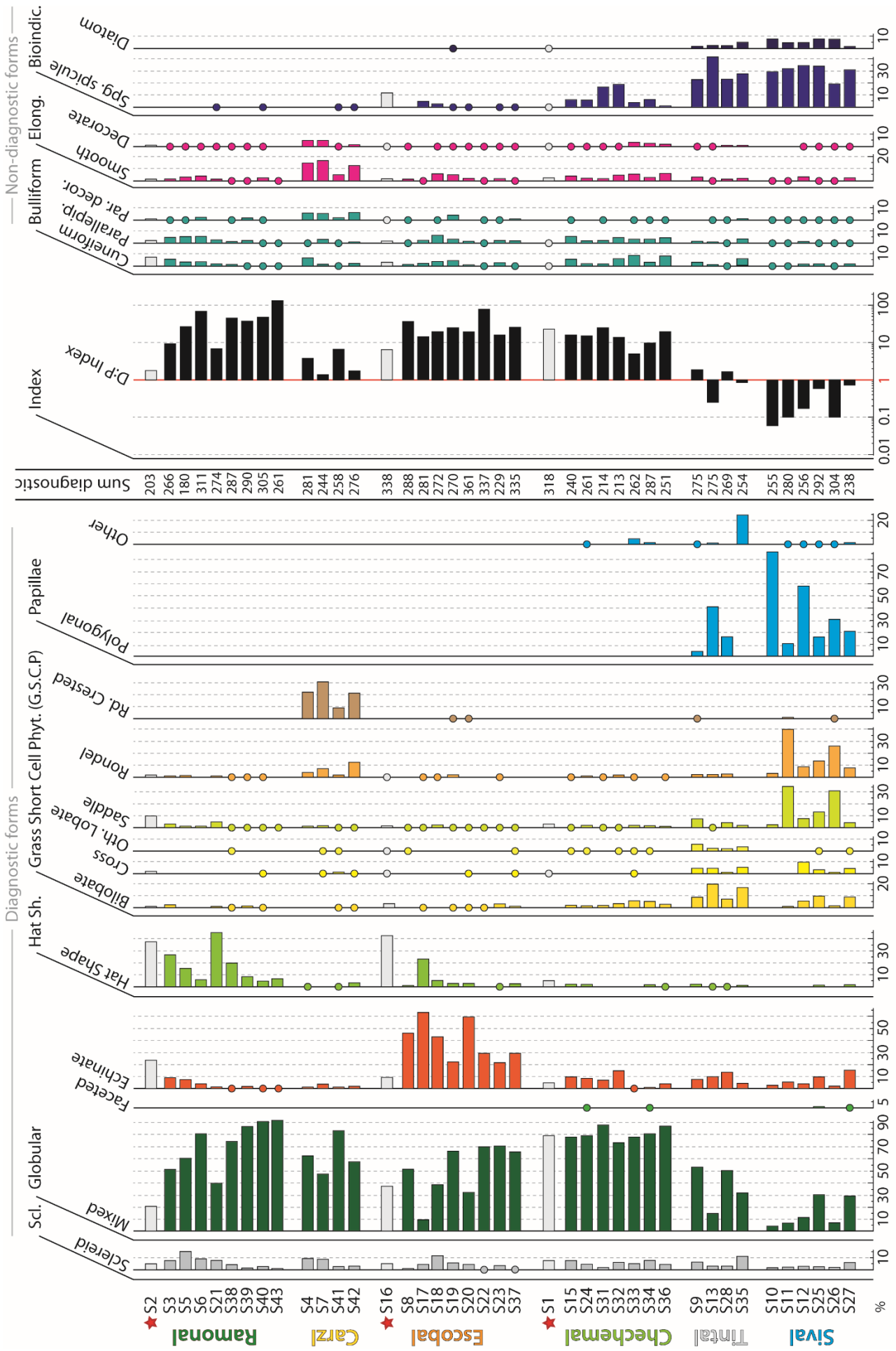
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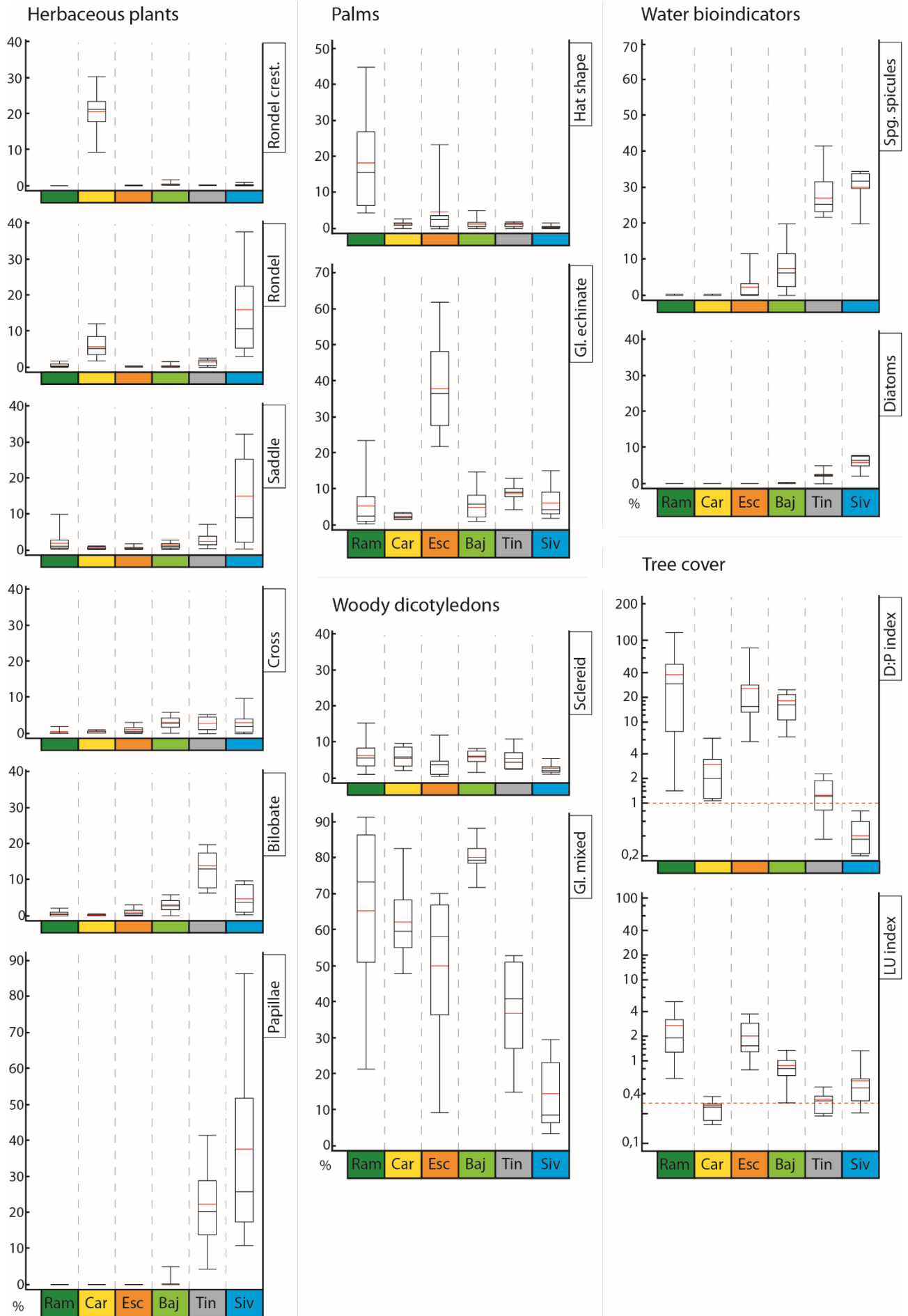
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1298 Fig. 6. Distribution diagram of phytolith morphotypes. (color)

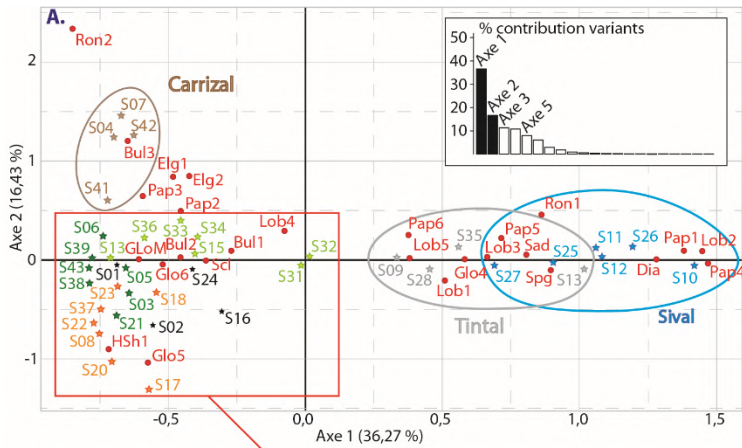


1300 Fig. 7. Statistical distribution of morphotypes by the environments. (color)

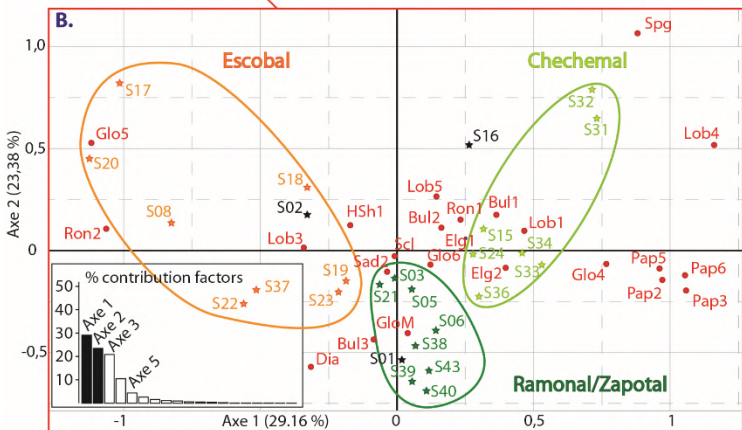


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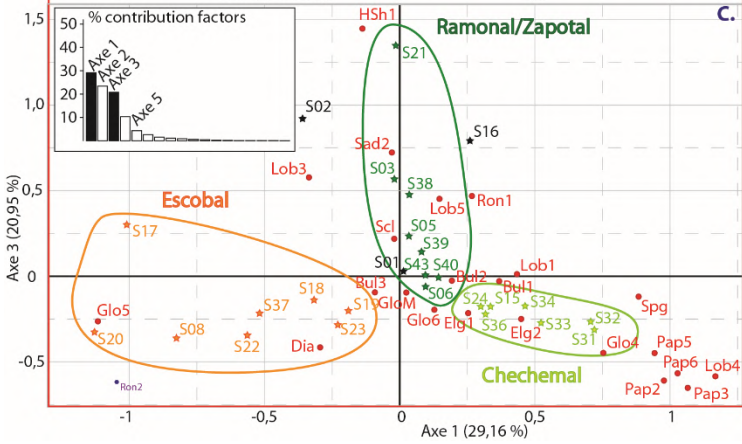
1302 Fig. 8. CA relating to the phytolith distribution diagram. (color)



Axe 1				Axe 2			
Variab.	Vb.	Crđ.	Ctrb.	Variab.	Vb.	Crđ.	Ctrb.
Sponge spi.	Spg	0,90	31,9 %	Rondel crest.	Ron2	2,37	25,5 %
Papillae pol.	Pap 4	1,47	16,6 %	Elongate smt.	Elg1	0,86	15,9 %
Diatom	Dia	1,28	8,4 %	Bulliform ech.	Bul3	1,23	9,1 %
Globular ech.	Glo5	-0,56	-4,3 %	Elongate dec.	Elg2	0,87	4,5 %
Globular mix.	GloM	-0,62	-16,6 %	Hat shape	Hsh1	-0,90	-11,5 %
				Globular ech.	Glo5	-1,04	-31,2 %



Axe 1				Axe 2			
Variab.	Vb.	Crđ.	Ctrb.	Variab.	Vb.	Crđ.	Ctrb.
Sponge spi.	Spg	0,90	24,8 %	Sponge spi.	Spg	1,08	46,6 %
Globular ech.	Glo5	1,47	-64,8 %	Globular ech.	Glo5	0,49	16,1 %
				Globular mix.	GloM	-0,41	-33,8 %



Axe 1				Axe 2			
Variab.	Vb.	Crđ.	Ctrb.	Variab.	Vb.	Crđ.	Ctrb.
Sponge spi.	Spg	0,88	24,8 %	Hat shape	Hsh1	1,44	83,2 %
Globular ech.	Glo5	-1,11	-64,8 %	Globular ech.	Glo5	-0,26	-5,0 %

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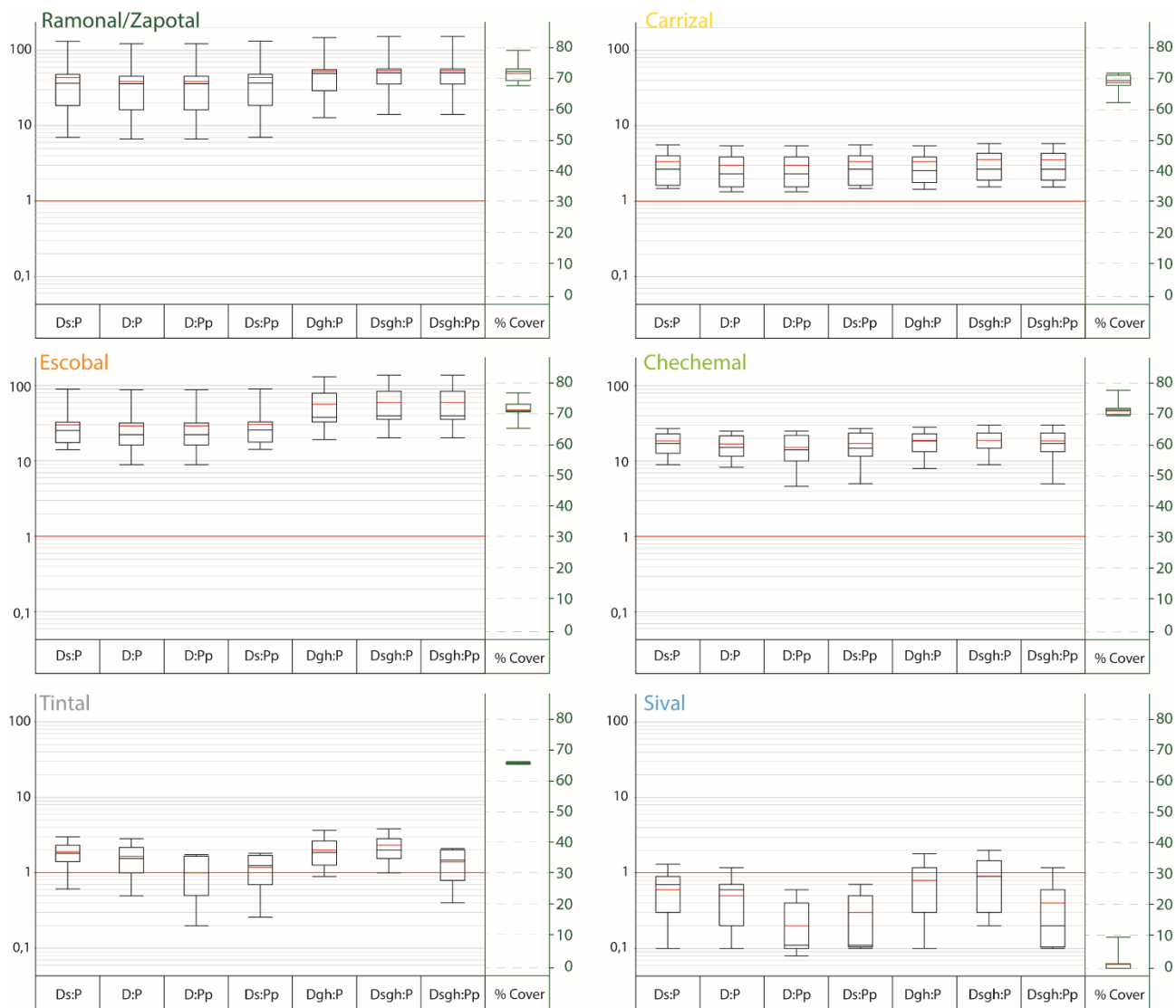
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1310 Fig. 9. Evolution of D/P values by environments and quadrats according to the D/P index formulas
 1311 used (Table 2) and vegetation cover. (color)



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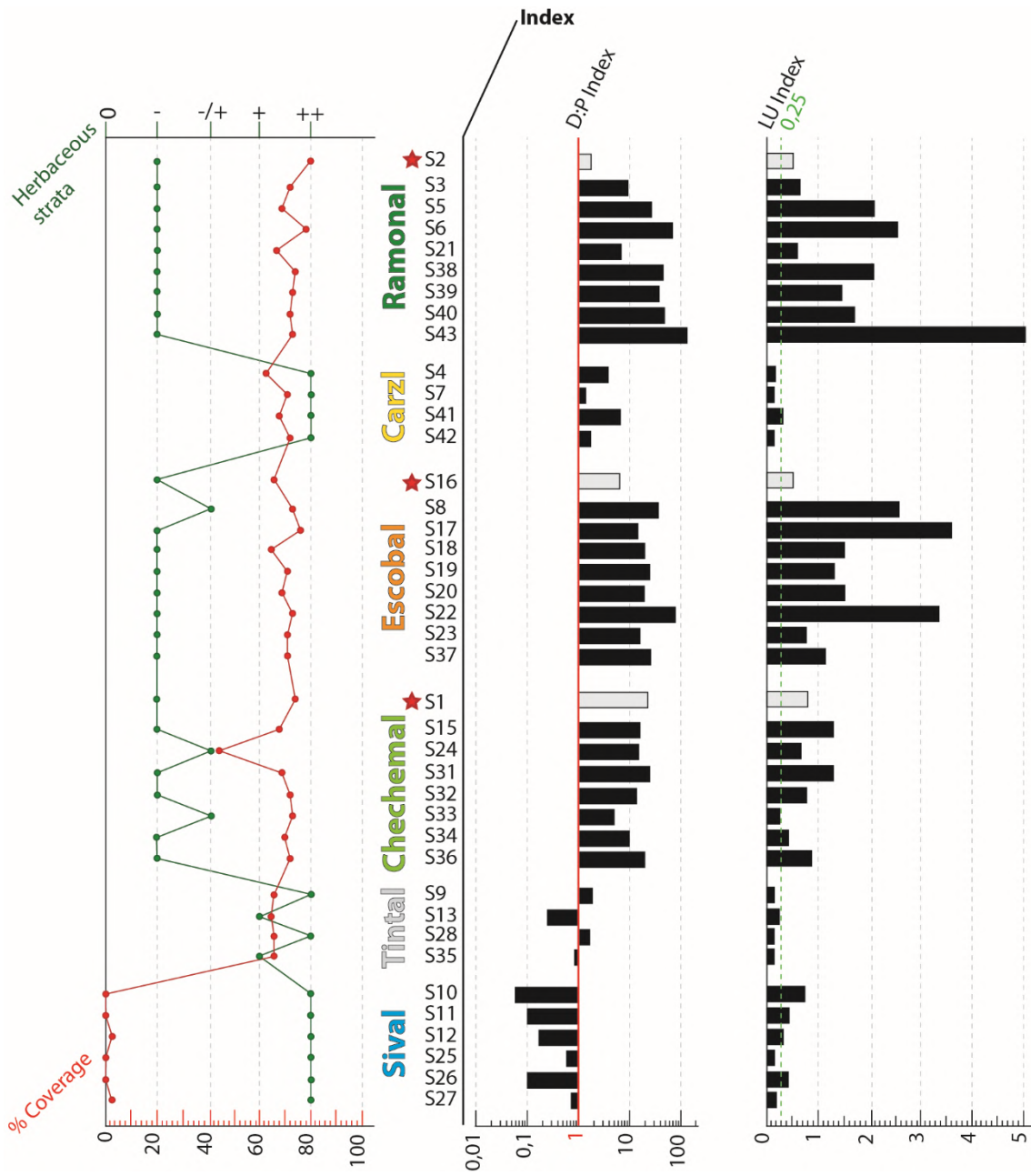
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1321 Fig. 10. Evolution of the LU index as a function of the D/P index, the vegetation cover rate and the
 1322 relative frequency of a grassy undergrowth. (color)



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1331 Tab.1: Classification of phytoliths encountered according to the Petén botanical families. Work to
1332 observe phytolith morphotypes in current plants: 1. [Mulholland, 1989](#); 2. [Ollendorf et al., 1988](#); 3.
1333 [Kealhofer & Piperno, 1998](#); 4. [Piperno & Pearsall, 1998b](#); 5. [Thorn, 2004](#); 6. [Lu et al., 2006](#); 7.
1334 [Piperno, 2006](#); 8. [Barboni & Bremond, 2009](#); 9. [Honaine et al., 2009](#); 10. [Iriarte & Paz, 2009](#); 11.
1335 [Mercader et al., 2009](#); 12. [Eichhorn et al., 2010](#); 13. [Watling & Iriarte, 2013](#); 14. [Neumann et al.](#)
1336 [2017](#); 15. [Collura & Neumann, 2017](#); 16. [Novelo et al. 2018](#). Classification work of phytolith forms
1337 in modern and ancient soils and sediments: 1. [Alexandre et al. 1997](#); 2. [Runge, 1999](#); 3. [Stromberg,](#)
1338 [2004](#); 4. [Neumann et al., 2009](#); 5. [Garnier et al., 2013](#); 6. [Dickau et al., 2013](#); 7. [Watling et al.,](#)
1339 [2016](#). Dicots (Anar. = Anacardiaceae, Apoc. = Apocynaceae, Aral. = Araliaceae, Bign. =
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. = arecoideae, cory. = coryphoideae); Cype. = Cyperaceae; Poac.
1346 = Poaceae (bamb. = bambusoideae, ehrh. = ehrhartoideae, pooi. = pooideae, arun. = arundinoideae,
1347 chlo. = chloridoideae, pani. = panicoideae).

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Cod.	Morphological description	Plt.	Trees																				
			Dicots.	Anar.	Apoc.	Aral.	Bign.	Bora.	Burs.	Capp.	Cele.	Clus.	Euph.	Faba.	Laur.	Malp.	Malv.	Melia.	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 irregular 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																				
ScL.1	Elongated shape, linear or twisted, with facets		5,6	15																			
ScL.2	Irregular shape covered by branches in relief		7		16	10																	3
ScL.3	Irregular shape covered with pointed ornamentation		2,3,6,7	15																			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	3	4	11																15
Glo.1	Spherical to sub-spherical shape with no visible ornamentation	I e	2,4,5,7	15	3	3	15	13	15	11,13	13												13
Glo.2	Sub-spherical shape with a rough, warty, or coarse surface	I f-g	1,2,3,4,5,6,7	13			13																13
Glo.3	Spherical to subspherical shapes grouped in the form of a complex	I h	5																				3
Glo.4	Big shape with an ornamented surface by large polygonal faces	I d					2																
Glo.5	Sub-spherical shape with a surface covered by thorns	I i-k																					
Hsh.1	Hemispherical shape covered with thorns	I l																					

Cod.	Trees	Herbs	Arac.	Arec.	Arec.	Palms	Cype.	Herbs										
								Poac.	bamb.	ehrh.	pooi.	arun.	chlo.	pani.				
Pap.1							2,5,7,9,13,16 2,6,9,13,2 2,6,9,10,13,2,4											
Pap.2																		
Pap.3																		
Pap.4																		
Pap.5																		
Pap.6																		
Lob.1										3	4,8,13,1	8	1,4	1,4,1	1,4,8,1,4	1,4,6,8,13,14,1,4,5,6,7		
Lob.2										3	8,10,14,4,6,7		1,4	4,1	1,4,8,1	1,4,6,13,14,1,4,5,7		
Lob.3										6	4,8,1		1,4	4,1	1,4,8,1	1,4,6,13,14,1,4,5,7		
Lob.4													1,4,8	1,8	8	8,4,5		
Lob.5											7,8		1,4,8	1,8	1,7,8,13,14,5,6,7			
Sad.											4,6	8	1,5	1,4,4	1,4,8,13,1,6,7	1,4		
Sad.1											10				4,5			
Sad.2															4,6,7,14,4,5			
Sad.3														4	14			
Sad.4																		
Ron.															1,4,8,3,4,5	1,4,8	1,4,8	
Ron.1															5,6	13	13	
Ron.2															5			
Scl.																		
Scl.1																		
Scl.2																		
Scl.3																		
Scl.4																		
Scl.5																		
Glo.1																		
Glo.2		15																
Glo.3																		
Glo.4																		
Glo.5																		
Hsh.1																		

1364 Table 2 Different formulas used to calculate the D/P index

	Index D:P Formula
Ds:P	$(\text{globular mixed} + \text{sclereid}) / (\text{GSCP})$
D:P	$(\text{globular mixed}) / (\text{GSCP})$
D:Pp	$(\text{globular mixed}) / (\text{GSCP} + \text{papillae})$
Ds:Pp	$(\text{globular mixed} + \text{sclereid}) / (\text{GSCP} + \text{papillae})$
Dgh:P	$(\text{globular mixed} + \text{globular echinate} + \text{hat-shape}) / (\text{GSCP})$
Dsgh:P	$(\text{globular mixed} + \text{sclereid} + \text{globular echinate} + \text{hat-shape}) / (\text{GSCP})$
Dsgh:Pp	$(\text{globular mixed} + \text{sclereid} + \text{globular echinate} + \text{hat-shape}) / (\text{GSCP} + \text{papillae})$

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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	<i>Ficus aurea</i> Nutt.						
	<i>Ficus cotinifolia</i> Kunth				+	-	
	<i>Ficus obtusifolia</i> Kunth						
Bakelac	<i>Laetia thammia</i> L.	++	++	-			
Canizte	<i>Pouteria campechiana</i> (Kunth) Baehni	+			-		
Caoba	<i>Swietenia macrophylla</i> King				-	-	
Catalox	<i>Swartzia cubensis</i> (Britton & Wilson) Standl.	-					
Cedro	<i>Cedrela odorata</i> L.	-	-				
Ceibal	<i>Ceiba pentandra</i> (L.) Gaertn.				-		
Chalteco	<i>Caesalpinia velutina</i> (Britton & Rose) Standl.						
	<i>Caesalpinia violacea</i> (Mill.) Standl.	+	+		-		
Chechem negro	<i>Metopium brownei</i> (Jacq.) Urb.				O	-	
Chicozapote	<i>Manilkara zapota</i> (L.) P.Royen	O	++	++	++		
Copal	<i>Protium copal</i> (Schltdl. & Cham.) Engl.	++	++	-	-		
Guaya	<i>Melicoccus oliviformis</i> Kunth	++		-	-		
Huevo de caballo	<i>Tabernaemontana donnell-smithii</i> Rose ex J.D.Sm.	-			-		
Jabin	<i>Piscidia piscipula</i> (L.) Sarg.	-		-	++		
Jobillo	<i>Astronium graveolens</i> Jacq.	+					
Jobo	<i>Spondias mombin</i> L.	++	++	+	+		
K'olo'k	<i>Talisia floresii</i> Standl.	+	+	+	-		
Limonaria	<i>Trichilia minutiflora</i> Standl.				-		
Maculiz	<i>Tabebuia heterophylla</i> (DC.) Britton				-		
	<i>Tabebuia rosea</i> (Bertol.) Bertero ex A.DC						
Madre de Cacao	<i>Gliricidia sepium</i> (Jacq.) Walp.				-		
Malerio blanco	<i>Aspidosperma megalocarpon</i> Müll.Arg.	+++	++	++	-		
Manchiche	<i>Lonchocarpus castilloi</i> Standl.	-		-			
Mano de leon	<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	-	-				
Matapalo	<i>Clusia flava</i> Jacq.	-					
Palo de gusano	<i>Caesalpinia yucatanensis</i> Greenm.						
	<i>Lonchocarpus guatemalensis</i> Benth.				-		
Palo de jiote	<i>Bursera simaruba</i> (L.) Sarg.	+	-	-	-		
Pimienta	<i>Pimenta dioica</i> (L.) Merr.	++	++	++	-		
Ramón	<i>Brosimum alicastrum</i> Sw.	O	++	++	+		
Ramón colorado	<i>Trophis racemosa</i> (L.) Urb.	-	-	-	-		
Roble	<i>Bourreria mollis</i> Standl.						
	<i>Ehretia tinifolia</i> L.				-	++	
Siricote	<i>Cordia dodecandra</i> A.DC.					-	
Tempisque	<i>Sideroxylon floribundum</i> (Lundell) T.D.Penn.	-					
Testap	<i>Guettarda combsii</i> Urb.	-					
Tinto	<i>Haematoxylum campechianum</i> L.				++	O	
Yasnic	<i>Vitex gaumeri</i> Greenm.			+	O	-	
Zapote,	<i>Manilkara chicle</i> (Pittier) Gilly						
	<i>Pouteria amygdalina</i> (Standl.) Baehni						
	<i>Pouteria belizensis</i> (Standl.) Cronquist						
	<i>Pouteria durlandii</i> (Standl.) Baehni						
	<i>Pouteria glomerata</i> (Miq.) Radlk.	O	++	++	+		
	<i>Pouteria reticulata</i> (Engl.) Eyma						
	<i>Pouteria viridis</i> (Pittier) Cronquist						
	<i>Sideroxylon stevensonii</i> (Standl.) Standl. & Steyerf.						
<i>Sideroxylon tepicense</i> (Standl.) T.D.Penn.							
SHRUB c / > 8	Arozillo	ind.			++		
	Cacho de toro	ind.			-	+	

	Cascarillo	<i>Croton guatemalensis</i> Lotsy <i>Croton reflexifolius</i> Kunth					-	O	-
	Chaya	<i>Cnidioscolus aconitifolius</i> (Mill.) I.M.Johnst.	++	+	++	-			
	Chechem blanco	<i>Cameraria latifolia</i> L.				-	+		
	Cordoncillo	<i>Piper amalago</i> L. <i>Piper psilorhachis</i> C.DC.	O	++	++	-			
	Guayavillo	<i>Eugenia axillaris</i> (Sw.) Willd. <i>Eugenia capuli</i> (Schltdl. & Cham.) Hook. & Arn. <i>Eugenia ibarrae</i> Lundell <i>Eugenia tikalana</i> Lundell						+++	
	Jiesmo	<i>Acacia angustissima</i> (Mill.) Kuntze <i>Acacia dolichostachya</i> S.F.Blake <i>Lysiloma acapulcense</i> (Kunth) Benth.				-	-	-	++
	Katsin	<i>Acacia gaumeri</i> S.F.Blake <i>Acacia riparia</i> Kunth				-	-	-	+
	Laurel	<i>Nectandra coriacea</i> (Sw.) Griseb. <i>Nectandra sanguinea</i> Rol. ex Rottb.	+			-	-	-	
	Majagua	<i>Hampea tomentosa</i> (C.Presl) Standl. <i>Hampea trilobata</i> Standl. <i>Mortoniendron guatemalense</i> Standl. & Steyerl.							++
	Manzanita	<i>Malpighia glabra</i> L. <i>Malpighia lundellii</i> C.V. Morton				-	-	-	
	Mora	<i>Maclura tinctoria</i> (L.) D.Don ex Steud.						++	+
	Nanze	<i>Byrsonima bucidifolia</i> Standl. <i>Byrsonima crassifolia</i> (L.) Kunth						+	
	Palo de Hormigas	<i>Alvaradoa amorphoides</i> Liebm.				-		-	
	Piñón	<i>Jatropha curcas</i> L.				-		-	
	Quebrahacha	<i>Wimmeria bartlettii</i> Lundell <i>Wimmeria concolor</i> Cham. & Schltdl.				-			
	Subin	<i>Acacia collinsii</i> Saff. <i>Acacia cornigera</i> (L.) Willd.					-	+	+++
	Zarza	<i>Mimosa pigra</i> L.							O
	Zikiya	<i>Chrysophyllum mexicanum</i> Brandegees <i>Chrysophyllum oliviforme</i> L.					+	-	
m.									
PALMS	Bayal	<i>Desmoncus chinantlensis</i> Liebm. ex Mart.				-	-	+	
	Cambray	<i>Chamaedorea seifrizii</i> Burret	++					++	++
	Escobo	<i>Cryosophila stauracantha</i> (Heynh.) R.J.Evans <i>Sabal mauritiiformis</i> (H.Karst.) Griseb. & H.Wendl.	++					O	+
	Guano / Botan	<i>Sabal mexicana</i> Mart.	+	+				O	+
	Xate	<i>Chamaedorea oblongata</i> Mart. <i>Chamaedorea elegans</i> Mart.				O	++	+	+
	Bejuco de aro	<i>Bignonia aequinocialis</i> L.				-			
	Calabaza de raton	<i>Cucurbita radicans</i> Naudin							++
HERBS	Carrizo	<i>Rhipidocladum bartlettii</i> (McClure) McClure						O	
	Lechuga	<i>Pistia stratiotes</i> L.							O
	Mozote ambra	<i>Teucrium vesicarium</i> Mill.							++
	Mozote macho	<i>Triumfetta semitriloba</i> Jacq.							++
	Navajuella	Cyperaceae ind.						-	++
	Tres marias	<i>Forchhammeria trifoliata</i> Radlk. ex Millsp.				-		-	+
	Tul'	<i>Cyperus articulatus</i> L.							O
	Yerba buena	<i>Mentha × piperita</i> L.							O
Zakate ambra	<i>Panicum trichanthum</i> Nees							++	

Zakate de huecht	<i>Rhynchospora cephalotes</i>					+	
Zakate I	<i>Olyra latifolia</i> L.	+++	++	++	++	++	
Zakate II	<i>Kyllinga pumila</i> Michx.					+	+
Zakate III	<i>Cyperus ochraceus</i> Vahl					+	+
Zakate IV	<i>Leptochloa virgata</i> (L.) P.Beauv.					-	-
Zakaton	<i>Phragmites australis</i> (Cav.) Trin. ex Steud.						O
Zakaton II	Poaceae ind.						+

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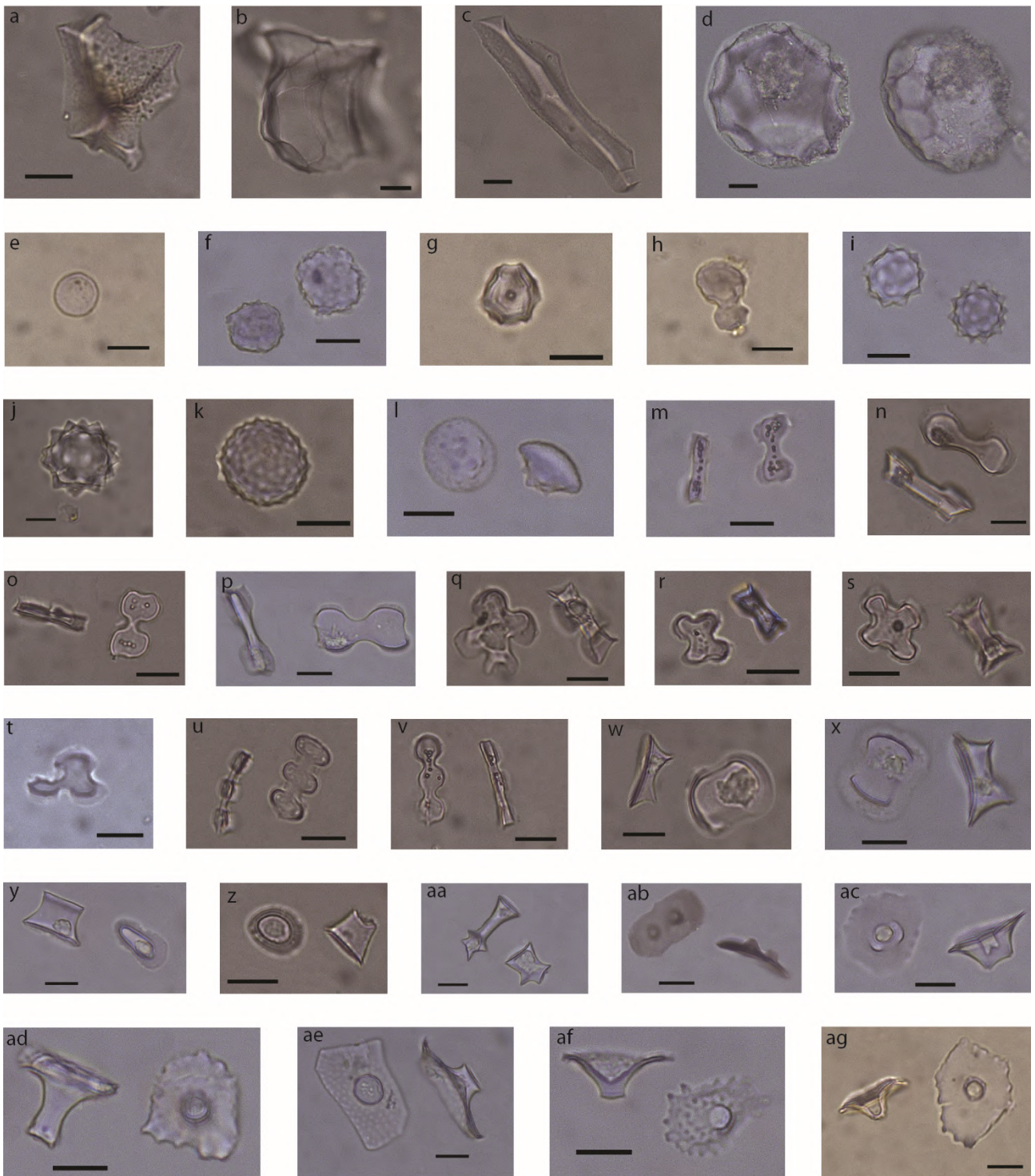
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1433 Plate I Main morphotypes of diagnostic phytoliths: a-c: sclereid, d: globular faceted, e: globular

1434 psilate, f-g: globular decorate, h: globular composed, i-k: globular echinate, l: hat-shape, m-p:

1435 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).



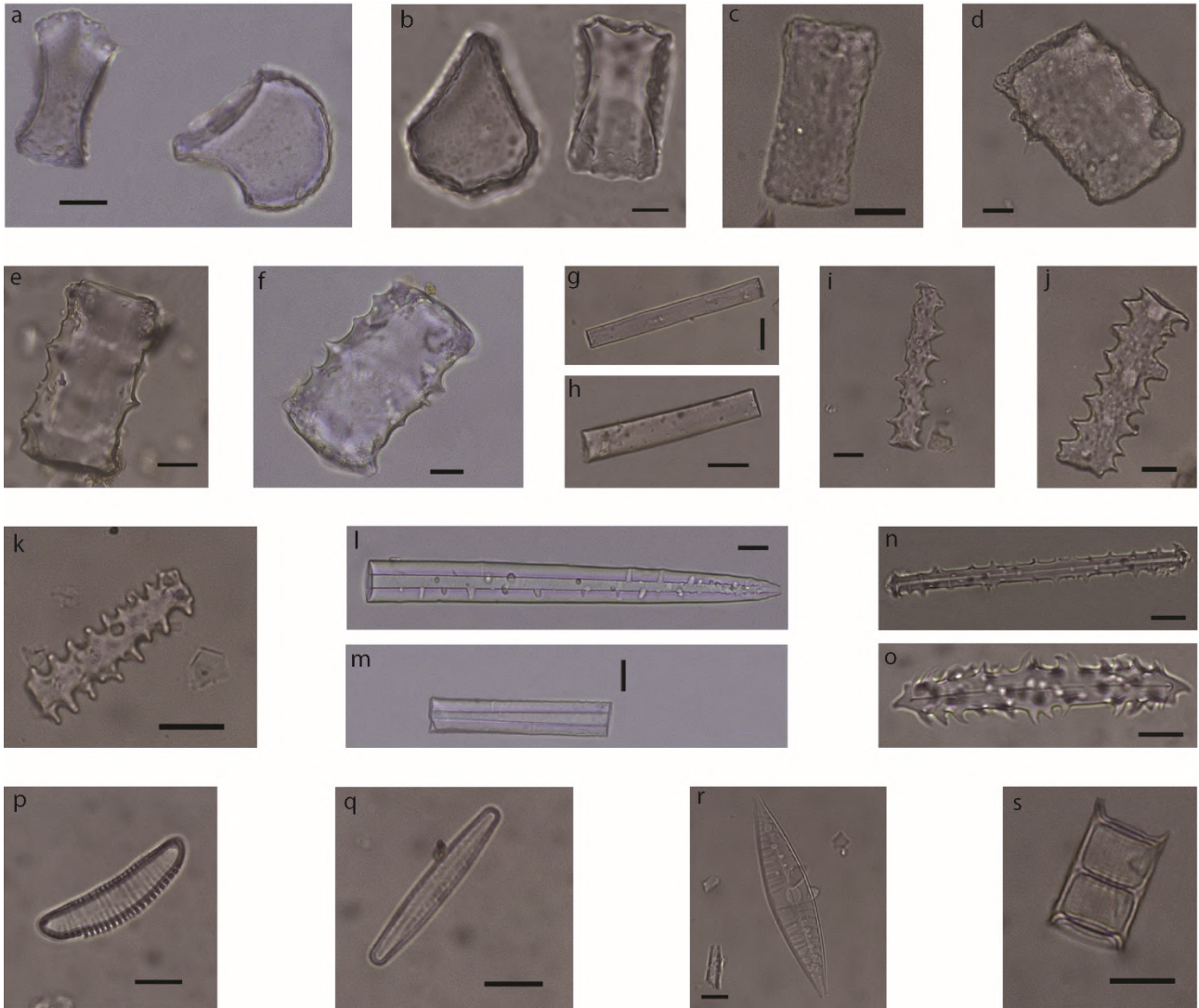
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1440 Plate II Main morphotypes of non-diagnostic phytoliths. a-b: bulliform cuneiform, c-d: bulliform

1441 psilate, e-f: bulliform decorate, g-h: elongate psilate, i-k: elongate decorate, l-o: sponge spicules, p-

1442 s: diatoms. (color)



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1451 Plate III Plant communities of the Naachtun territory. a: Ramonal/Zapotal, b: Carrizal, c: Escobal,
 1452 d: Chechemal, e: Tintal, f: Sival. (color)

Ramonal/Zapotal



Carriçal



Escobal



Chechemal



Tintal



Sival



1453