Natural and human-mediated drivers of microevolution in Neotropical palms: a historical genomics approach

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Abstract

- Microevolution in Amazonia has been far less documented than in temperate regions and still constitutes a major knowledge gap. Moreover, the actual influence of pre-Columbian societies through the Holocene remains unclear, although it could provide interesting insights on the relationship between natural and human-mediated evolutionary processes in driving microevolution.
- Because they are widespread and traditionally managed since pre-Columbian times, Neotropical palms are choice models to investigate the drivers of microevolution in Amazonia. In this study, we carried out a preliminary exploration of the genomic diversity in two pairs of congeneric palm species in French Guiana (*Astrocaryum* spp. and *Oenocarpus* spp.).
- We built upon an original sampling design, taking into account both regional climate variations and local-scale pre-Columbian occupation, and designed a new target capture kit of 20,000 molecular probes scattered across exonic regions of more than 5,000 nuclear genes in Arecoïdeae ("ARECO5000+"). Hundreds of palm libraries were sequenced through Illumina sequencing, providing a unique – high-coverage – genomic dataset in these non-model species.
- We explored patterns of genomic diversity and differentiation within and across populations, bringing state-of-the-art knowledge about the roles of climate adaptation and pre-Columbian domestication. By documenting original cases of "incipient" domestication, these pioneer results open new avenues toward a better understanding of microevolution in Amazonia and of the impact of pre-Columbian societies on present-day biodiversity patterns.

Key word: *Oenocarpus* spp., *Astrocaryum* spp., targeted capture, Illumina sequencing, climate adaptation, pre-Columbian societies, ring ditch, incipient domestication.

Introduction

Evolution in Amazonia has been far less documented than in temperate regions and still constitutes a major knowledge gap. Evolutionary studies in Amazonia also largely concentrated on macroevolution through long-term geological periods, providing interesting insights onto speciation and extinction dynamics in relation to landscape changes associated with the Andean uplift and the formation of the Amazon river (Hoorn et al. 2010), to species dispersal abilities (B. T. Smith et al. 2014) and to biotic interactions (Onstein et al. 2018). On the contrary, less attention has been paid to the microevolution of plants and animals during the Quaternary (Cavers and Dick 2013), and even less during the Holocene. This period, which started about 11,000 years ago, experienced both a global warming subsequent to the last glacial period resulting in the present climate, and the establishment of dense networks small-scale human societies subsequent to the human colonization of South America in late Pleistocene (Llamas et al. 2016; Rothhammer and Dillehay 2009). A better understanding of the drivers of plant and animal evolution during the Holocene could thus bring interesting insights on the interactions between natural and human-mediated evolutionary processes and their role shaping present-day patterns of biodiversity.

Neotropical palms of the Arecoideae subfamily are choice models to investigate the drivers of microevolution in Amazonia. Dated phylogenies revealed that Arecoideae crown node diversified in mid-Cretaceous in South America, suggesting a Neotropical origin (Baker and Couvreur 2013). Today, Neotropical palms are widespread in Amazonia ; Arecaceae standing at the second position of the most abundant plant families in forest tree inventories with some “hyperdominant” species (ter Steege et al. 2013). Neotropical palms also constitute a key resource to human societies since pre-Columbian times, whose multiple uses – including

subsistence food and building materials – have been extensively documented at least since the 1850's (Wallace 1853; N. Smith 2015). Surprisingly, they are also particularly abundant at archaeological sites with evidence of long-term human occupation, and some species (in particular *Astrocaryum* spp. and *Oenocarpus* spp.) are commonly credited as 'biological indicators' of ancient settlements (Odonne et al. 2019).

This is notably the case at the so-called "ring ditches" that are abundant in interfluvial terra-firme forests in lowland Amazonia, from Bolivia (John F Carson et al. 2015) to French Guiana (Petitjean Roget 1991). These pre-Columbian earthworks provide valuable evidence of anthropogenic disturbances, with belowground enrichments in pre-Columbian ceramics, organic matter and charcoals characterizing "anthropogenic soils" that are commonly attributed to slash-and-burn agriculture (Bodin et al. 2020; Brancier et al. 2014). Even if the actual magnitude of land use at these sites remain controversial – with hypotheses varying from extensive forest clearance to the exploitation of naturally open savanna (Watling et al. 2017; John Francis Carson et al. 2014) – there is no more doubt that pre-Columbian societies have strongly impacted forest landscapes, thus contrasting with previous depictions of Amazonia as an undisturbed, primary forest (Levis et al. 2017).

These repeated and converging observations feed the long-standing hypothesis that many plant species, including Neotropical palms, may have been "incipiently-" or "semi-" domesticated through pre-Columbian times (Clement 1999; Clement et al. 2010, 2006). Whether pre-Columbian societies have actually shaped patterns of palm diversity through domestication, and how human-mediated processes interacted with natural ones, remain however largely unknown. This knowledge gap is primarily underpinned by a profound lack of observational genomic data in non-model Neotropical species that we intend to fill in this study.

We carried out a preliminary exploration of the genomic diversity in two pairs of congeneric Neotropical palms in coastal French Guiana: *Astrocaryum paramaca* and *A. sciophilum* on one side, *Oenocarpus bacaba* and *O. bataua* on the other side. We sampled populations following an original sampling design taking into account both regional and local-scale evolutionary processes related to climate variations and pre-Columbian occupation, respectively. At the regional scale, we sampled populations in study sites with contrasted rainfall to catch climate adaptation. At the local scale, we sampled palms both on the top of ring ditches and in the surrounding forests to catch the impact of domestication associated with local anthropogenic disturbances. We designed a new capture kit composed of 20,000 molecular probes to target exonic regions within thousands of nuclear genes, and carried out an extensive targeted-capture experiment and next-generation sequencing (NGS) of hundreds of libraries.

Here, we introduce this new capture kit ("ARECO5000+") and provide new NGS data on the state and distribution of genomic diversity in Neotropical palms in coastal French Guiana. We investigate intra-specific patterns of diversity and differentiation driven by both neutral evolutionary processes (gene flow and admixture) and selective ones, disentangling the roles of (natural) climate adaptation and of (human-mediated) pre-Columbian domestication that operated at the different spatial scales.

Materials and Methods

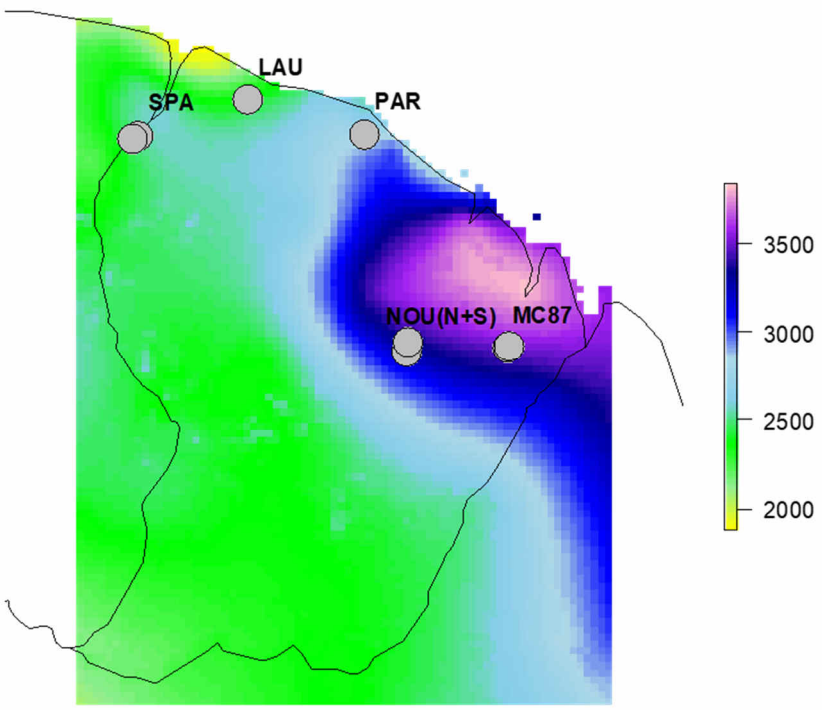
1. Palm species

We focused on four palm species that belong to the Arecoideae sub-family and that are widespread in forest landscapes of French Guiana: two species of the genus *Astrocaryum* (*A. paramaca* and *A. sciophilum*) and two species of the genus *Oenocarpus* (*O. bacaba* and *O. bataua*). *Oenocarpus bacaba* and *O. paramaca* are pan-Amazonian species that are broadly distributed from Colombia to north Brazil. *Oenocarpus bataua* stands at the 7th position amongst the 20 most abundant species in the Amazonian tree flora, while *O. bacaba* stands at the 33th position (ter Steege et al. 2013). The distribution of *A. paramaca* and *A. sciophilum* is restricted to northeast Amazonia (Suriname, French Guiana and Brazil, GBIF Secretariat: GBIF Backbone Taxonomy. https://doi.org/10.15468/39omei). Despite this, *A. sciophilum* stands at the 51th position amongst the most abundant species in forest tree inventories. Moreover, *O. bacaba* and *A. sciophilum* are two biological indicators of pre-Columbian settlements in French Guiana, as their abundance is significantly higher in forest plots with evidence of strong pre-Columbian anthropogenic disturbances than in natural plots (Odonne et al. 2019). *Astrocaryum* spp. and *Oenocarpus* spp. are major sources of food and of building and handicraft materials in Amazonia (Sosnowska et al. 2015; Cummings and Read 2016). Their leaves are traditionally used in basketry and to build houses (see for example maloca's walls and roof, García et al. 2015; Davy 2007; Fadiman 2008; Coomes 2004; Gutierrez 2020; Kahn 1993), while their fruits are used to make oil (*e.g.* 'seje' oil) and beverages (*e.g.* so called 'comou' and 'wassaï' in French Guiana and 'bacaba wine' in Northwest Amazonia, Cunha et al. 2019; Castro et al. 2014; Puerari et al. 2015).

2. Sampling strategy

130 Palm populations of the four palms species were sampled in five study sites in the coastal
131 French Guiana with different rainfall ranging from about 2400 to 3500 mm.year^{-1} (**Figure 1**):
132 three archaeological sites with ring ditches (SPA, MC87 and NOU), plus two additional
133 undisturbed sites without evidence of pre-Columbian occupation (LAU and PAR). In the three
134 study sites with ring ditches, we sampled palm populations both at the top of the ring ditches
135 and in the surrounding (undisturbed) forest (< 5 km from the ring ditch), **Table 1**. When the
136 species were present, we collected a piece of leaf for 20 to 100 adult palms per species in each
137 sampling site and local condition (pre-Columbian occupation "+" and "–").

138



139

140 **Figure 1**. Localization of the study sites and annual precipitation (in mm.year^{-1}) in French
141 Guiana. Current precipitations were extracted from WorldClim version 1 using R (libraires
142 "`raster`" and "`sp`") and are representative of the period 1960-1990
143 (http://www.worldclim.com/version1).

144 **Table 1.** Localization of populations in the different sampling sites and local conditions of pre-
145 Columbian occupation. "+" refers the top of the ring ditch with evidence of pre-Columbian
146 occupation, and "–" refers the surrounding sampling forest area without evidence of pre-
147 Columbian occupation. "Nouragues North" and "Nouragues South" indicate the localization of
148 two ring ditches in the north and in the south of the Nouragues Ecological research station,
149 respectively. Coordinates are provided in decimal degrees (WGS84).

Study site	Site ID	Local condition	Latitude (N)	Longitude (E)	Rainfall (mm.year^{-1})
Sparouine	SPA	–	5.272861999	-54.22715197	2529
	SPA	+	5.253569037	-54.253331	2491
Laussat	LAU	–	5.479205009	-53.59530601	2391
Paracou	PAR	–	5.279138032	-52.92425998	2818
Nouragues South	NOU_S	–	4.038217971	-52.68241298	3246
	NOU_S	+	4.029483022	-52.681869	3246
Nouragues North	NOU_N	–	4.081238005	-52.67338903	3299
	NOU_N	+	4.079981977	-52.67142003	3299
Montagne Couronnée 87	MC87	–	4.053646959	-52.09517601	3517
	MC87	–	4.05699201	-52.086698	3517

150

151 ### 3. Probes design, targeted capture and sequencing

152 We took advantage of the availability of the chromosome-level reference genome for the oil
153 palm (*Elaeis guineensis*, Arecaceae, Arecoideae) to design a custom of capture kit of 20,000
154 molecular probes located within 5,209 orthologous nuclear genes scattered across all 16
155 chromosomes ("ARECO5000+"). Details on probes design is provided in **Supplementary**
156 **material 1**. Probe sequences are available upon request from the corresponding author. The
157 probes were then synthetized by Daicel Arbor Biosciences (myBaits Custom DNA-Seq©).
158 Molecular experiments were further performed at the AGAP genotyping platform (Montpellier,
159 France). Plant DNA was extracted from 15 mg of dried leaves. Ten to fifteen best-quality DNAs

per population were retained for library preparation, targeted-capture and sequencing, resulting in the sampling design described in **Table 2** and totaling 405 libraries (one per palm). Genomic library preparation for multiplexed individuals and targeted capture by bait hybridization followed published protocols (Rohland and Reich 2012; Mascher et al. 2013) with some modifications. The molecular protocol is provided in **Supplementary material 2**. Briefly, for each genotype a genomic barcoded library was built; 48 barcoded libraries were mixed together for the capture by hybridization using the myBaits Custom DNA-Seq© kit "ARECO5000+". Libraries of *Oenocarpus bataua* were sequenced (paired-end, 2 × 150bp) on an Illumina MiSeq at the AGAP genotyping platform (Montpellier, France), while libraries of *Astrocaryum* spp. and *Oenocarpus bacaba* were sequenced by the Get-PlaGe core facility (GenoToul platform, INRA Toulouse, France http://www.genotoul.fr) on an Illumina HiSeq3000. Sequence data are available on EMBL-ENA under accession PRJEB51800.

Table 2. Sampling design for library preparation and sequencing. "NA" indicates that the species was absent at this sites and/or local condition.

Site ID	Local condition	*Astrocaryum paramaca*	*Astrocaryum sciophilum*	*Oenocarpus bacaba*	*Oenocarpus bataua*
SPA	–	12	12	12	12
SPA	+	12	12	12	12
LAU	–	12	12	12	12
PAR	–	12	12	12	12
NOU_S	–	12	NA	NA	NA
NOU_S	+	12	NA	12	12
NOU_N	–	15	10	NA	12
NOU_N	+	14	15	15	12
MC87	–	12	12	NA	12
MC87	+	12	12	NA	12
TOTAL		**125**	**97**	**75**	**108**

177 ## 4. Bioinformatics

178 **Reads demultiplexing and pre-processing.** Reads were demultiplexed based on their 6
179 nucleotide barcodes with `fastq-multx` of the `ea-utils-2.7` suit of tools (Aronesty
180 2013) with options `-b -x -m 0 -d 1`, and split into individual .fastq files (two files per
181 library, corresponding to "R1" and "R2" paired reads). Read sequences that failed to pass the
182 chastity filter (identified "Y" in the "@" line in CASAVA 1.8) were discarded using the
183 command:

```
184 zcat $lib_name.R1.fastq.gz | grep -A 3 '^@.* [^:]*:N:[^:]*:' |
185 grep -v "^--$" > $lib_name_pf.R1.fastq.
```

186 Reads were further cleaned using `FASTX-Toolkit (RRID:SCR_005534) v.0.0.14`:
187 they were trimmed with `fastx_trimmer` with option `-Q 33 -f 10 -l 140`, resulting
188 in reads of 140-nucleotide long. Individual bases of low quality (phred-score < 25) were then
189 masked with `fastq_masker` with options `-q 25 -Q 33`. At last, read 3'-end and 5'-end
190 were cut and orphan reads were discarded using `sickle-1.33` (Joshi and Fass 2011) with
191 options `pe -l 100` (*i.e.* default quality threshold of 20 and length threshold of 100bp). Once
192 cleaned, reads were quality controlled with `FastQC-0.11.5` (Andrews 2010).

193 **Mapping.** Cleaned reads of *Astrocaryum* spp. and *Oenocarpus* spp. libraries were mapped
194 separately against *Elaeis guineensis* reference genome (EG5) using `bwa` (H. Li and Durbin
195 2010, 2009): the reference was indexed with the command `bwa index` and paired-reads were
196 mapped using `bwa mem` with option `-t 10`.

197 Mapping were post-processed using `samtools-1.9` (H. Li 2011; H. Li et al. 2009).
198 Multiple mapped reads were discarded from .bam alignments using `samtools view` with
199 the command:

```
samtools view -h mapping.bam | awk '$17 !~ /XA:/ || $1 ~ /^@/' | /usr/local/samtools-1.9/bin/samtools view -bS > mapping_unique.bam
```

Alignments were then sorted and indexed using `samtools sort` and `samtools index`, respectively. Mapping statistics were computed using `samtools stats`, `samtools flagstat` and `samtools bedcov`. Sequencing and mapping statistics are provided in **Supplementary materials 3 and 4**.

Following a first mapping against *Elaeis guineensis* reference genome, the reference was updated by editing genus-specific consensus (one for *Astrocaryum* spp. and one for *Oenocarpus* spp.) to take into account the genomic divergence between *Elaeis guinensis* and the genera under study. This step aimed to avoid detecting polymorphisms caused by inter-genus variation in the following. This was achieved by calling variants using `samtools mpileup` with options `-uf` for each *Astrocaryum* spp. and *Oenocarpus* spp. alignments, respectively. The two consensus references were edited with `bcftools index` (v.1.3) and `bcftools consensus` (Danecek et al. 2021). Then, the libraries of each species (*Astrocaryum paramaca*, *A. sciophilum*, *Oenocarpus bacaba* and *O. bataua*) were mapped separately against the corresponding genus-specific consensus reference following the mapping procedure described above.

SNP and genotype calling. Variants were called using `samtools-1.9` and `bcftools-1.3`: genus-specific consensus were indexed with `samtools faidx` and variant were called with `samtools mpileup` with options `-g -t DP` followed by `bcftools call` with options `-vc`. The resulting .vcf file was filtered with `grep` to discard monomorphic sites, variants detected on unassembled scaffolds or chloroplast as well as indels to retain nuclear single-nucleotide polymorphisms (SNPs) only. SNPs were post-filtered with `R version 3.5.1` (R Core Team 2021) to retain SNPs and genotypes with a quality threshold of 20, and

225 a per-library coverage threshold of 6X. SNPs and genotypes that did not meet the criteria were
226 edited as missing ("NA"), and SNPs that became monomorphic or contained more than 20% of
227 missing values were discarded. This resulted in 178,358 and 23,252 high-quality SNPs in
228 *Astrocaryum* spp. and *Oenocarpus* spp., respectively. Last, palm samples with more than 20%
229 of missing values were discarded. The list of samples retained for genetic analyses is provided
230 in **Supplementary material 5**.
231

232 **5. Population genetics**

233

234 Genome-wide patterns of genetic structure and diversity were computed on a random subset
235 of 5,000 SNPs in `R version 3.5.1` (command `sample` with argument `replace =`
236 `F)`. Genotype tables were converted from tabular (data frame) to `genind` objects using the
237 function `df2genind` (package `adegenet`).
238 **Genetic differentiation.** Pairwise genetic differentiation (F_{ST}) was estimated both between
239 congeneric species and within each species. Weir and Cockerham's F_{ST} were estimated using
240 the function `genet.dist` (package `hierfstat`) with argument `method="WC84"`.
241 **Individual ancestry.** Genome-wide genetic structure was assessed for each species by
242 estimating individual ancestry (Frichot et al. 2014) with the function `snmf` (package `LEA`) with
243 arguments `ploidy = 2`, `entropy = TRUE` and `CPU = 8`. The genetic structure was
244 explored from `K=1` to `K=10` ancestral populations (*A. paramaca*), to `K=8` (*A. sciophilum*), to
245 `K=6` (*O. bacaba*) or to `K=9` (*O. bataua*). The most probable number of clusters was retained
246 based on cross-entropy criterion (lower values indicating better fit to the predictions) and each
247 palm sample was assigned to a given group with an ancestry threshold of 0.5.
248 **Isolation-by-distance.** Isolation-by-distance was tested across populations within each species
249 through Mantel tests between genetic and geographic distances. Genetic distance were

250 estimated with the function `dist.genpop` (package `adegenet`) with argument `method =`
251 `3` (*i.e.* coancestry coefficient or Reynolds' distance, Jombart 2008; Jombart and Ahmed 2011).
252 Geographic distances (euclidean) were computed from geographic coordinates using the
253 function `dist` with default arguments. Mantel tests between geographic and genetic distance
254 matrices were computed with the function `mantel.randtest` (package `ade4`, Mantel
255 1967; Thioulouse et al. 1997).

256 **Admixture tests.** Admixture between populations was evaluated through *f3* admixture tests for
257 all combinations of three populations (Patterson et al. 2012; Peter 2016; Reich et al. 2009):
258 $f_3(P_X ;P_A,P_B)$, where P_X is the target population and P_A and P_B are two source populations.
259 Admixture tests were encoded with `R version 3.5.1`. f_3 statistic was estimated following
260 the equation by Reich et al. (2009):

261 $$\mathbb{E}(p_X - p_a)(p_X - p_b),$$

262 where p_x, p_a and p_b are the allele frequencies in the populations P_X, P_A and P_B, respectively, and
263 $\mathbb{E}$ the expected value across all SNPs. Negative values indicate admixture between A and B.
264 The significance of f_3 was assessed by bootstrap (function `sample` with argument `replace`
265 `= T`) through 500 iterations. Z-scores were converted into p-values (left-tailed) with the
266 function `pnorm`.

267 **Intra-population diversity.** Observed (*Ho*) and expected heterozygosity (*He*) within each
268 species and populations was estimated with `adegenet` from `genind` objects. `Genind`
269 objects containing multiple populations were split into separate populations using the function
270 `seppop` and summary statistics were exported with the function `summary`. Whether *Ho* was
271 higher than *He* was assessed for each population through non-parametric Wilcoxon tests
272 (because of non-homogeneity of variances between *Ho* and *He*) with the function
273 `wilcox.test`. Inbreeding coefficients (*Fis*) were estimated following the formula: $Fis =$
274 $1 - \frac{Ho}{He}$. Hardy Weinberg equilibrium was tested for each SNP through Chi-squared tests with

275 the function `hw.test` (package `pegas`), and the proportion of SNPs showing significant
276 departure from HW equilibrium at a 1% threshold was assessed.
277 **Selection test.** We carried out a genome-wide scan for adaptive differentiation within each
278 species using `BayPass v.2.1`. Genotype data were converted into allele counts and
279 `BayPass` core model was run a first time using observed SNP counts as input. The number of
280 populations in each dataset was specified with option `-npop` and MCMC parameters were
281 specified with options `-nthreads 8 -thin 15 -burnin 2500 -npilot 15 -`
282 `pilotlength 5000`. The estimated covariance matrix (Ω), which provides an accurate
283 estimate of genome-wide allele frequency covariance across populations, was converted into a
284 correlation matrix in `R version 3.5.1` using the function `cov2cor`. The singular values
285 of the covariance matrix was decomposed using `svd` and left singular vectors (U) were
286 extracted to plot the genome-wide structure across populations. Pseudo-observed data (PODs)
287 of 10,000 SNPs (for *Oenocarpus* spp.) or 100,000 SNPs (for *Astrocaryum* spp.) were simulated
288 with the `simulate.baypass` function (`BayPass` miscellaneous R function), specifying
289 the total number of allele counts for each SNP (*i.e.* sample size) and the estimated
290 hyperparameters a_π and b_π (*i.e.* posterior mean and standard deviation of the Beta distribution
291 expressing the mean reference allele frequency, ~ancestral reference allele frequency) as input.
292 These PODs correspond to a simulated set of SNP counts that take into account the genome-
293 wide (neutral) genetic structure empirically inferred from observed SNPs counts. The core
294 model was run again using PODs as input under the same parameters to calibrate SNP-specific
295 statistics (standardized allele frequencies α^{std}, *XtX* and derived statistics) under neutral
296 hypothesis. `BayPass` outputs were post-processed with `R version 3.5.1.` The
297 robustness of the core model was assessed by evaluating the FMD distance (Förstner and
298 Moonen 2003) between covariance matrices estimated on observed data (Ω^{OBS}) and on
299 simulated data (Ω^{POD}) using `fmd.dist` function (`BayPass` miscellaneous R function). SNP-

300 specific departures from genome-wide (*i.e.* neutral) differentiation were detected based on the
301 joint distribution of:

302 - SNP-specific XtX_i (Günther and Coop 2013) estimated by `BayPass` (which describes
303 the differentiation across all populations for each SNP *i* explicitly corrected for genome-
304 wide covariance, whatever their regional and local environmental conditions), and
305 - two additional statistics (δ_i and Δ_i) derived from estimated standardized allele
306 frequencies ($\alpha_{i,j}^{STD}$, which describes allele frequencies for each SNP *i* within each
307 population *j* explicitly corrected for the genome-wide covariance matrix) and designed
308 to quantify variations in α^{STD} driven by climate adaptation and pre-Columbian
309 domestication, respectively.

310 Because α^{std} are unbounded, α^{std} were rescaled between 0 and 1 through min-max
311 normalization:

312 $$\alpha_{i,j}^{STD\ (OBS)} = \frac{\alpha_{i,j}^{STD\ (OBS)} - \min(\alpha^{STD})}{\max(\alpha^{STD}) - \min(\alpha^{STD})} \text{ and } \alpha_{i,j}^{STD\ (POD)} = \frac{\alpha_{i,j}^{STD\ (POD)} - \min(\alpha^{STD})}{\max(\alpha^{STD}) - \min(\alpha^{STD})},$$

313 where:

314 - $\alpha_{i,j}^{STD\ (OBS)}$ and $\alpha_{i,j}^{STD\ (POD)}$ are the standardized allele frequency at SNP *i* in population
315 *j* estimated from observed and simulated data respectively ;
316 - $\min(\alpha^{STD}) = \min\left(\alpha^{STD\ (OBS)}, \alpha^{STD\ (POD)}\right)$;
317 - $\max(\alpha^{STD}) = \max(\alpha^{STD\ (OBS)}, \alpha^{STD\ (POD)})$.

318 The statistic δ quantifies clines in α^{STD} along the regional precipitation gradient:

319 $$\delta_i = |\beta_i|.r_i^2 ,$$

320 where $|\beta_i|$ and r_i^2 are the absolute regression coefficient and the r-squared of the linear model
321 between allele frequency at SNP i and precipitation: $\alpha_{i,j}^{STD} = \beta_i.prec_j$, with $prec_j$ the

precipitation in population *j* (scaled between 0 and 1). Linear models were fitted for each SNP with the function `lm`.

The statistic Δ quantifies absolute differences in α^{STD} between contrasted local conditions of pre-Columbian occupation (+ *versus* –) within ($\Delta_{i,s}$) and across study sites (Δ_i):

$$\Delta_{i,s} = \left|\alpha^{STD}_{i,(j+)} - \alpha^{STD}_{i,(j-)}\right|,$$

and

$$\Delta_i = \sum_s (\Delta_{i,s})$$

where *j*+ and *j*– refer to populations located on the ring ditch and in the surrounding natural forest for each study site *s* (*i.e.* single-site contrast), respectively, and $\Delta_{i,s}$ is the sum across study sites *s* (*i.e.* multi-site contrast).

δ and Δ statistics where separately computed on observed data (δ_i^{OBS}, $\Delta_{i,s}^{OBS}$, Δ_i^{OBS}) and on PODs (δ_i^{POD}, $\Delta_{i,s}^{POD}$, Δ_i^{POD}). A SNP was retained as being shaped by climate adaptation if it was both over-differentiated across all populations whatever their local environment based on XtX at a 95% PODs threshold (*i.e.* condition 1), and if it displayed clinal allele frequency variation with regional precipitation based on δ at a 95% PODs threshold (*i.e.* condition 2). Similarly, a SNP was retained as being shaped by domestication if both condition 1 was met, and if it displayed local differences in allele frequencies in relation to pre-Columbian occupation based on Δ at a 95% PODs threshold (*i.e.* condition 3).

Climate adaptation SNP	**Domestication SNP**
Condition 1: $XtX_i^{OBS} > q_{(95)}(XtX_i^{POD})$	
Condition 2: $\delta_i^{OBS} > q_{(95)}(\delta_i^{POD})$	Condition 3: $\Delta_i^{OBS} > q_{(95)}(\Delta_i^{POD})$

where:

342 • XtX_i^{OBS} is the SNP-specific differentiation estimated on observed data, and
343 $q_{(95)}(XtX_i^{POD})$ the 95-quantile of the distribution (across all SNPs) of SNP-specific
344 differentiation estimated on simulated data ;
345 • δ_i^{OBS} is the SNP-specific cline in allele frequency along the regional precipitation
346 gradient estimated on observed data, and $q_{(95)}(\delta_i^{POD})$ the 95-quantile of the distribution
347 (across all SNPs) of SNP-specific clines in allele frequency along the regional
348 precipitation gradient estimated on simulated data ;
349 • Δ_i^{OBS} is the SNP-specific difference in allele frequency between local conditions of pre-
350 Columbian occupation (+ *versus* –) estimated on observed data, and $q_{(95)}(\Delta_i^{POD})$ the
351 95-quantile of the distribution (across all SNPs) of SNP-specific differences in allele
352 frequency between local conditions of pre-Columbian occupation estimated on
353 simulated data.

354 **Outlier blastn.** Last, we retrieved the identity of genes containing precipitation and adaptation
355 SNPs. For each species, we extracted the sequences of the genomic regions surrounding each
356 outlier SNP (+/- 200 bp) from consensus genomic sequences using `bedtools getfasta`
357 (`bedtools-2.27.1`). Each SNP-surrounding region was then blasted against the NCBI
358 nucleotide database using `blastn` (`NCBI BLAST+ v. 2.10.1+`), limiting blast search by
359 taxonomy (*Elaeis guineensis* taxid = 51953 and *Phoenix dactylifera* taxid = 42345) and
360 returning the first good hit to optimize computation time.

361

Results

1. Genome-wide genetic structure and differentiation

Genetic differentiation. At the inter-specific level, pairwise F_{ST} across populations ranged between 0.30 and 0.55 in *Astrocaryum* spp. and between 0.23 and 0.30 in *Oenocarpus* spp. Intra-specific F_{ST} ranged between 0.003 and 0.4 in *A. paramaca*, between 0.01 and 0.11 in *A. sciophilum*, between 0 and 0.06 in *O. bacaba* and between 0 and 0.01 in *O. bataua*, **Figure 2** and **Supplementary material 6 (Tables S5.1 & S5.2)**. In *A. paramaca*, the population originating from the undisturbed area close to the ring ditch in MC87 (i.e "MC87–") showed a surprisingly high differentiation with all other population of this species ranging between 0.39 and 0.40, while the differentiation between all other populations ranged between 0 and 0.28.

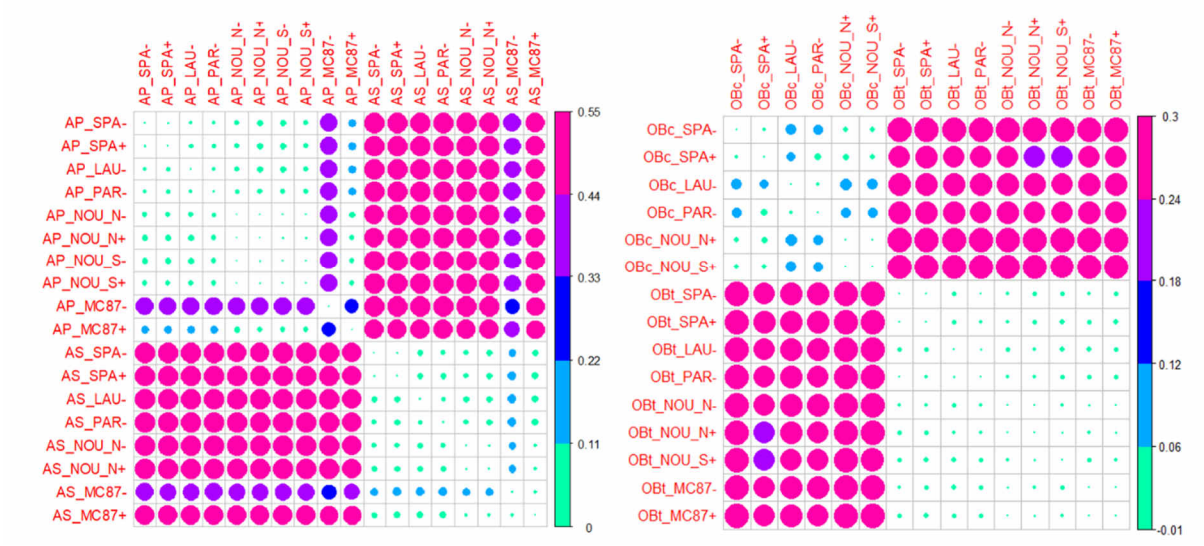


Figure 2. Correlation plots showing patterns of genome-wide genetic differentiation across populations of *Astrocaryum* spp. (left) and *Oenocarpus* spp. (right). "AP" refers to *A. paramaca*, "AS" to *A. sciophilum*, "OBc" to *O. bacaba* and "OBt" to *O. bataua*.

Individual ancestry. Cross-entropy criterion of individual ancestry was lower for K=3 and K=4 in *A. paramaca* and *A. sciophilum*, respectively, and for K=4 and K=2 in *O. bacaba* and *O.bataua*, respectively, thus indicating a genome-wide genetic structuring at a grain lower than the species level (**Supplementary material 6, Figures S6.1 & S6.2**). Within each species, the genetic structure was consistent with the regional location of the palm populations from west to east, **Figure 3**.

In *A. paramaca*, we detected one cluster in the west (in red) including all individuals from the sites of Sparouine (SPA), Laussat (LAU) and Paracou (PAR), and two genetic clusters in the east (sites of NOU and MC87), with all individuals associated to the blue group originating from MC87.

In *A. sciophilum*, we detected two genetic clusters in the west: one corresponding to the study site SPA (in green) and one (in purple) corresponding to the study sites LAU and PAR. In the east (NOU and MC87), most individuals were assigned to the light blue group. Few individuals originating from MC87 were assigned to a fourth group (in red). In addition, one individual was assigned to the purple group and one ambiguous individual was not assigned to any group.

In *O. bacaba*, we detected three genetic groups in the west, and one in the east. The palms from SPA were in majority assigned to the light blue group, while the populations from LAU and PAR included palms assigned to both light blue and red groups. The third group (green) corresponded to two individuals originating from the ring ditch (+) of SPA. The palms from NOU were all assigned to the fourth group (purple).

In *O. bataua*, we detected two groups with one group (purple) including palms from SPA and PAR, and another group (blue) including palms from NOU and MC87 except one palm in the latter that clustered with the purple group with an ancestry coefficient slightly above 0.5. In LAU, quite all palms clustered with the blue group except two palms clustered with the purple group.

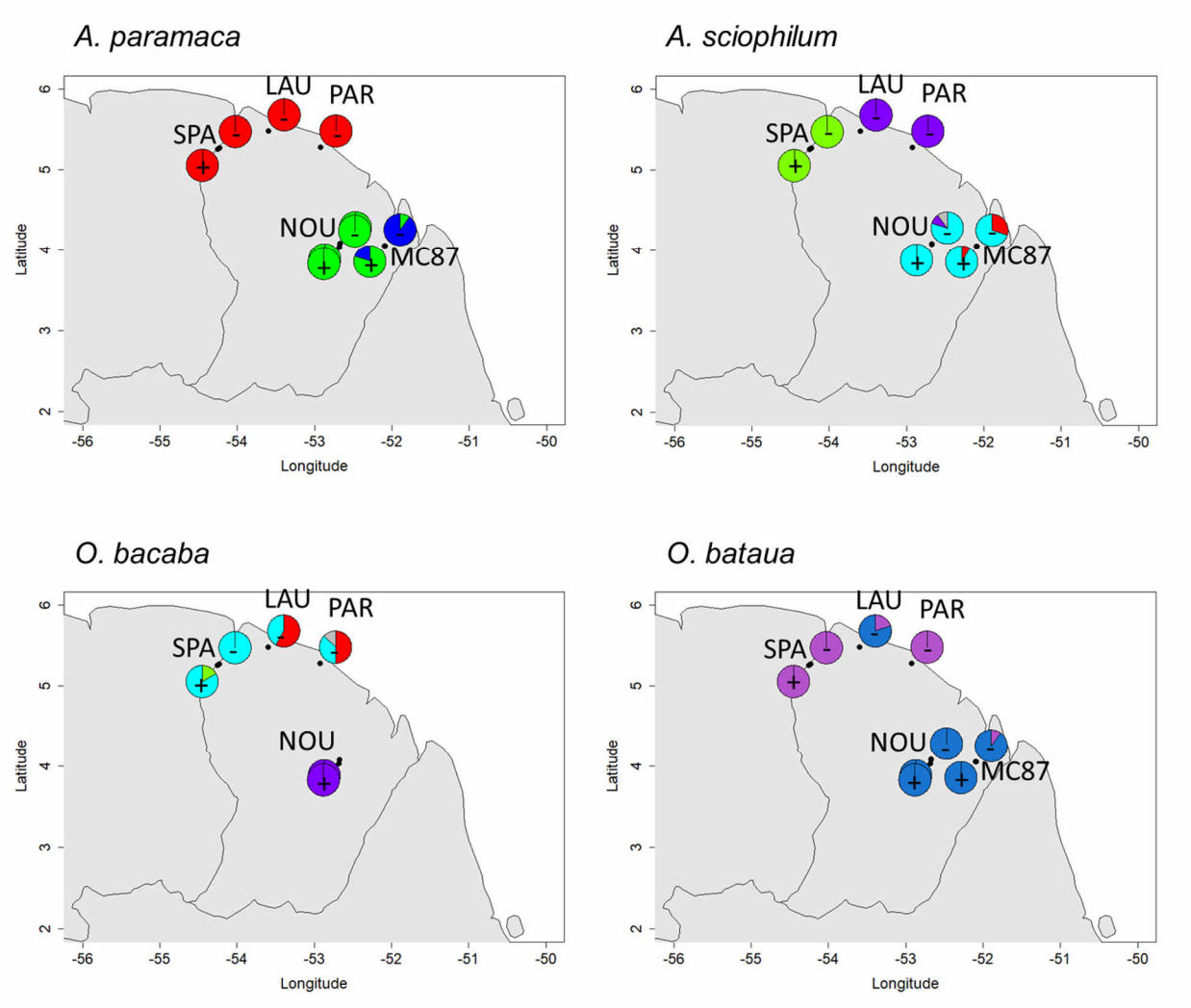


Figure 3. Geographic genetic structure. The pies indicate the proportion of individuals assigned to genetic each cluster within each study site and local condition of pre-Columbian occupation. Grey slices indicate ambiguous individuals that cannot be assigned to a given group with an ancestry coefficient > 0.5.

Isolation-by-distance. Patterns of isolation by distance were significant in *A. sciophilum* (p-value = 0.001) and *O.bataua* (p-value = 0.002), but not in *A. paramaca* (p-value = 0.20) nor in *O. bacaba* (p-value = 0.14). In *A. paramaca*, however, IBD became significant (p-value = 0.003) after exclusion of populations from MC87 (MC87 + and MC87–), **Supplementary material 6 (Figure S6.3)**.

414 **Admixture.** Significantly negative f_3 statistics were detected at a threshold of 5% for four target
415 populations of *Astrocaryum* spp. (*A. paramaca* from MC87 +, *A. sciophilum* from MC87 + and
416 MC87 – and *A. paramaca* from NOU_N –), and for one target population *of Oenocarpus* spp.
417 (*O.bacaba* in SPA +), **Supplementary material 6 (Figure S6.4)**. Populations of *A. paramaca*
418 from MC87 + appeared to be admixed between populations of *A. paramaca* from NOU (N and
419 S, + and –) and populations of *A. paramaca* from MC87 –, while *A. paramaca* from NOU_N –
420 appeared to be admixed between *A. paramaca* from NOU_S – and *A. sciophilum* from NOU_N
421 (+ and –), LAU – and/or PAR, thus suggesting patterns of inter-specific hybridization between
422 *A. paramaca* and *A. sciophilum* in the study site of NOU. Similar patterns of inter-specific
423 admixture also appeared in *A. sciophilum* from MC87 (+ and –), revealing admixture between
424 *A. sciophilum* from NOU_N (+ and –) and *A. paramaca* from MC87 –. *Oenocarpus bacaba*
425 from SPA + also appeared to be admixed between *O. bacaba* from SPA – and *O. bataua* from
426 different sites.

427 **Intra-population diversity.** In *Astrocaryum* spp., observed heterozygosity (*Ho*) ranged
428 between 0.136 (*A. sciophilum* in MC87 +) and 0.163 (*A. paramaca* in NOU_S –). In
429 *Oenocarpus* spp., *Ho* ranged between 0.351 (*O. bacaba* SPA – and LAU – ; *O.bataua* NOU_S
430 +, SPA – and PAR –) and 0.372 (*O. bacaba* SPA+). *Fis* was negative, indicating outcrossing.
431 *Fis* was slightly higher in *A. paramaca* than in *A. sciophilum* although non-significant
432 (Wilcoxon p-value = 0.1), and higher in *O. bacaba* than in *O. bataua* (Wilcoxon p-value =
433 0.0004), **Table 3** and **Supplementary material 6 (Figure S6.5)**. In *Astrocaryum* spp., *Fis* was
434 higher in the populations from MC 87 where it became non-significantly negative. *Fis* also tend
435 to be slightly higher in populations on ring ditches (+) than in surrounding natural populations
436 (–) in *Astrocaryum* spp. and *O. bataua* while the trend was opposite in *O. bacaba*, **Table 3** and
437 **Supplementary material 6 (Figure S6.5)**. A large proportion of SNPs shew significant
438 departure from HW equilibrium with large variations across populations ranging from 7% to

439 12% in *A. paramaca*, from 0 % and 14% in *A. sciophilum*, from 18% to 27% in *O. bacaba* and

440 between 0 and 25% in *O.bataua*.

441 **Table 3.** Intra-population diversity statistics (*He*, *Ho* and *Fis*) in *Astrocaryum* spp. with

442 Wilcoxon tests for differences between *Ho* and *He* (** : p-value <0.01 ; * : p-value<0.05).

	Ho	***He***	***Fis***
A. paramaca			
SPA –	0.156 (sd=0.292)	0.105	-0.333 (sd=0.381) **
SPA +	0.156 (sd=0.294)	0.105	-0.337 (sd=0.396) **
LAU –	0.160 (sd=0.301)	0.107	-0.365 (sd=0.401) **
PAR –	0.157 (sd=0.294)	0.106	-0.345 (sd=0.389) **
NOU_N –	0.165 (sd=0.290)	0.114	-0.273 (sd=0.362) **
NOU_N +	0.162 (sd=0.289)	0.112	-0.288 (sd=0.372) **
NOU_S –	0.163 (sd=0.296)	0.110	-0.340 (sd=0.371) **
NOU_S +	0.162 (sd=0.292)	0.111	-0.312 (sd=0.371) **
MC87 –	0.140 (sd=0.285)	0.104	-0.141 (sd=0.587)
MC87 +	0.154 (sd=0.278)	0.128	-0.101 (sd=0.556)
A. sciophilum			
SPA –	0.143 (sd=0.303)	0.089	-0.496 (sd=0.408) **
SPA +	0.139 (sd=0.289)	0.092	-0.384 (sd=0.407) *
LAU –	0.137 (sd=0.287)	0.090	-0.403 (sd=0.400) *
PAR –	0.137 (sd=0.285)	0.091	-0.363 (sd=0.402) *
NOU_N –	0.144 (sd=0.292)	0.094	-0.383 (sd=0.389) **
NOU_N +	0.137 (sd=0.285)	0.091	-0.366 (sd=0.405) *
MC87 –	0.137 (sd=0.257)	0.142	0.030 (sd=0.614) *
MC87 +	0.136 (sd=0.272)	0.110	-0.004 (sd=0.625)

443

444 **Table 4.** Intra-population diversity statistics (*He*, *Ho* and *Fis*) in *Oenocarpus* spp. with

445 Wilcoxon tests for differences between *Ho* and *He* (** : p-value <0.01 ; * : p-value<0.05).

	Ho	***He***	***Fis***
O. bacaba			
SPA –	0.352 (sd=0.415)	0.205	-0.575 (sd=0.389) **
SPA +	0.373 (sd=0.393)	0.228	-0.438 (sd=0.408) **
LAU –	0.351 (sd=0.381)	0.226	-0.427 (sd=0.436) **
PAR –	0.356 (sd=0.385)	0.228	-0.453 (sd=0.442) **
NOU_N +	0.353 (sd=0.411)	0.207	-0.535 (sd=0.400) **
NOU_S +	0.351 (sd=0.413)	0.206	-0.554 (sd=0.398) **
O. bataua			
SPA –	0.351 (sd=0.428)	0.198	-0.659 (sd=0.367) **
SPA +	0.353 (sd=0.427)	0.200	-0.639 (sd=0.376) **

LAU –	0.352 (sd=0.430)	0.198	-0.700 (sd=0.347) **
PAR –	0.352 (sd=0.427)	0.200	-0.686 (sd=0.353) **
NOU_N –	0.358 (sd=0.427)	0.203	-0.644 (sd=0.375) **
NOU_N +	0.361 (sd=0.423)	0.206	-0.614 (sd=0.384) **
NOU_S +	0.357 (sd=0.424)	0.204	-0.631 (sd=0.378) **
MC87 –	0.355 (sd=0.421)	0.204	-0.617 (sd=0.376) **
MC87 +	0.353 (sd=0.422)	0.202	-0.642 (sd=0.365) **

2. SNP-specific differentiation

`BayPass` core model provided accurate estimates of genome-wide genetic structure, SNP-specific differentiation (XtX_i) and derived statistic designed to disentangle footprints of divergent selection caused by precipitation (δ_i) at the regional scale, and pre-Columbian occupation (*i.e.* domestication) at the local scale (Δ_i). Covariance matrices estimated on observed data (Ω^{OBS}) were close to covariance matrices estimated on pseudo-observed data (Ω^{POD}), with $\overline{FMD}$ = 1.06 in *A. paramaca*, $\overline{FMD}$ = 1.25 in *A. sciophilum*, $\overline{FMD}$ = 2.07 in *O. bacaba* and $\overline{FMD}$ = 2.9 in *O. bataua*, **Supplementary material 6 (Figures S6.6 to S6.9)**. The genome-wide genetic structure estimated by `BayPass` through covariance matrices was also consistent with the genetic structure estimated by `snmf` through individual ancestry, confirming the robustness of `BayPass` to empirically infer the genomic structure across populations **Supplementary material 6 (Figures S6.6 to S6.10)**. We further detected SNPs displaying patterns of differentiation related to precipitation and/or pre-Columbian occupation based on the joint distribution of XtX_i and derived statistics (δ_i and Δ_i), **Figure 4** and **Supplementary material 6 (Figure S6.11)**.

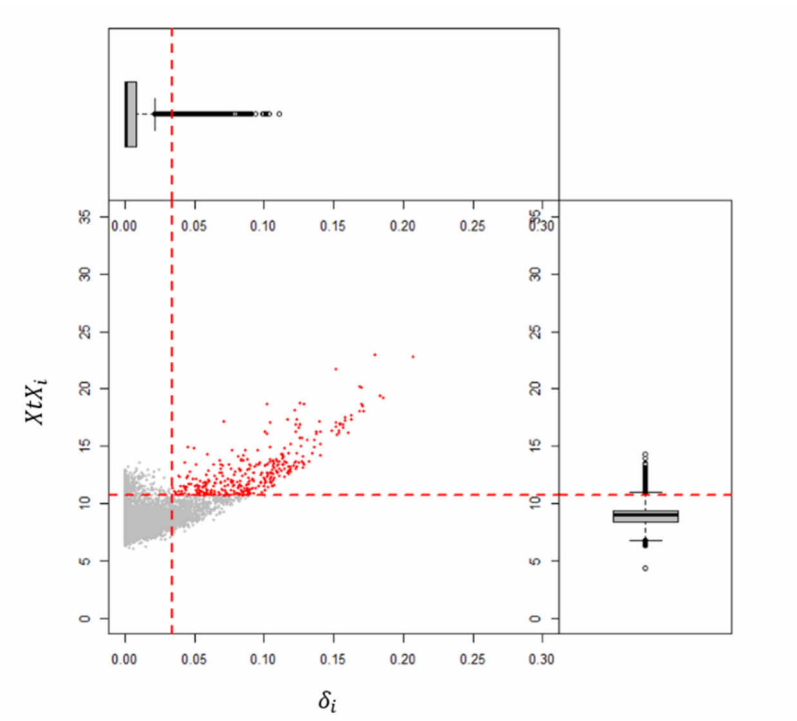


Figure 4. Example of SNP detection in relation to precipitation in *Oenocarpus bataua* based on the joint distribution of XtX_i and δ_i.

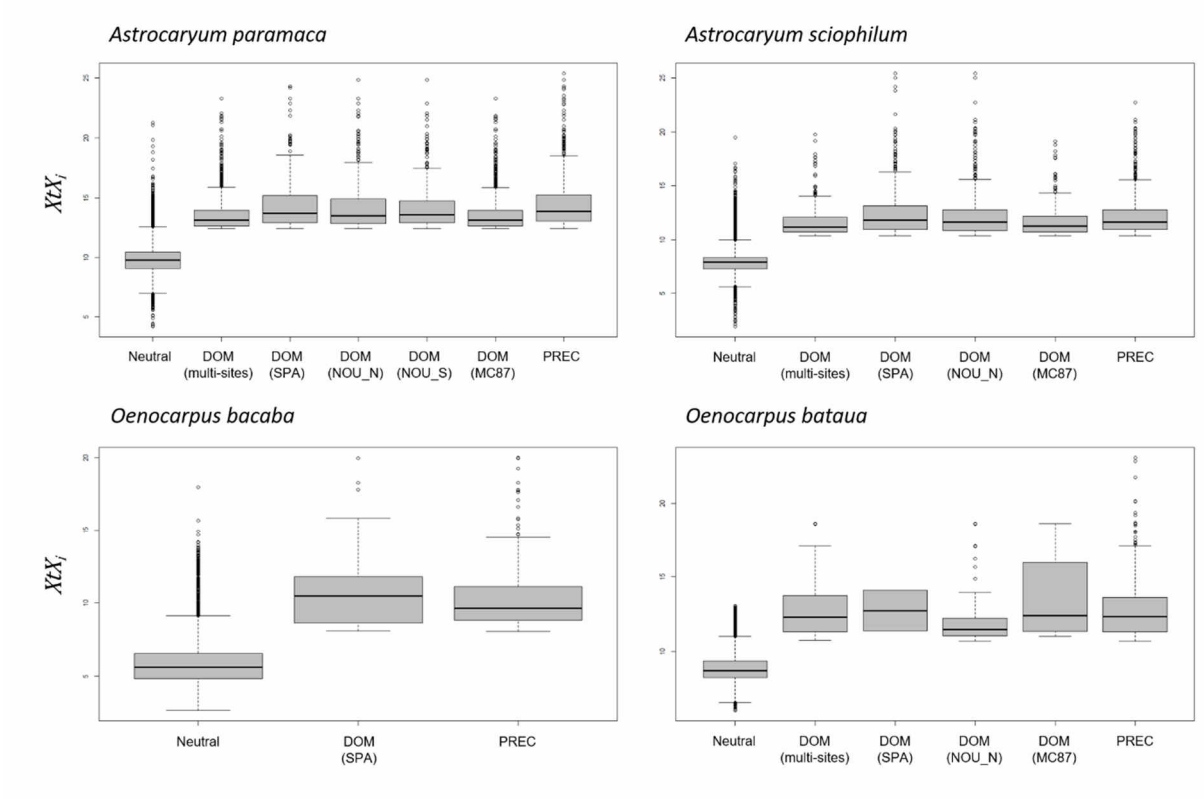
Between 0.74% (*A. sciophilum*) and 1.42% (*O. bataua*) climate adaptation SNPs were detected in the different species, and between 0.20% (*O. bataua*) and 1.25% (*A. paramaca*) domestication SNPs across all study sites. Moreover, the proportion of domestication SNPs was higher when considering all sites together (i.e. multi-site contrast) than within each site (single-site contrast), with many SNPs detected in one or two study sites only. Nevertheless, many domestication SNPs were shared between study sites: in *A. paramaca*, 1,252 domestication SNPs were detected in two sites, 285 were detected in three sites, and 28 in four sites ; in *A. sciophilum*, 564 SNPs were detected in two sites and 105 in three sites ; in *O. bataua*, only 10 SNPs were detected in two sites. The number of shared SNPs between pairs of study sites is provided in **Supplementary material 6 (Tables S6.3 to S6.6).**

476 **Table 5.** Number of over-differentiated SNPs detected in the four species in relation to climate
477 adaptation and domestication (out of 178,358 SNPs in *Astrocaryum* spp. and 23,252 SNPs in
478 *Oenocarpus* spp.). Because *O. bacaba* was only present on the ring ditches in NOU_N and
479 NOU_S and was absent from MC87, the detection of domestication SNP was based on a single
480 contrast in SPA.

	A. paramaca	***A. sciophilum***	***O. bacaba***	***O. bataua***
Climate adaptation SNPs				
Across all populations and sites	1345 (0.75%)	1320 (0.74%)	297 (1.25%)	331 (1.42%)
Domestication SNPs				
Across sites (multi-site contrast)	2238 (1.25%)	386 (0.22%)	NA	47 (0.20%)
Within sites (single-site contrast)				
• *SPA*	624 (0.35%)	640 (0.36%)	284 (1.22%)	2 (0.01%)
• *NOU N*	679 (0.38%)	810 (0.45%)	NA	70 (0.30%)
• *NOU S*	623 (0.35%)	NA	NA	NA
• *MC87*	2212 (1.24%)	374 (0.21%)	NA	16 (0.07%)

481

482 The median of SNP-specific differentiation (XtX_i) for neutral SNPs was 9.8 (Q90 = [8.6 ; 12.0])
483 in *A. paramaca*, 8.0 ([6.7 ; 9.9]) in *A. sciophilum*, 5.6 ([4.5 ; 8.1]) in *O. bacaba* and 8.7 ([7.6 ;
484 11.0]) in *O. bataua*. XtX_i ranged between 9.6 ([8.2 ; 14.6]) in *O. bacaba* and 13.9 ([12.5 ; 18.1])
485 in *A. paramaca* for climate adaptation SNP, and between 10.48 ([8.2 ; 13.8]) in *O. bacaba* and
486 13.1 ([12.5 ; 16.0]) in *A. paramaca* without differences in the extent of genetic differentiation
487 between climate adaptation and domestication SNPs, **Figure 6**.



488

489 **Figure 6.** Distribution of SNP-specific differentiation (XtX_i) in neutral SNPs, domestication

490 (DOM) and climate adaptation SNPs (PREC).

491

492 Interestingly, several SNPs shew variations in allele frequency in relation to both precipitation

493 and pre-Columbian occupation (**Supplementary material 6**, **Tables S6.3 to S6.6**)), allowing

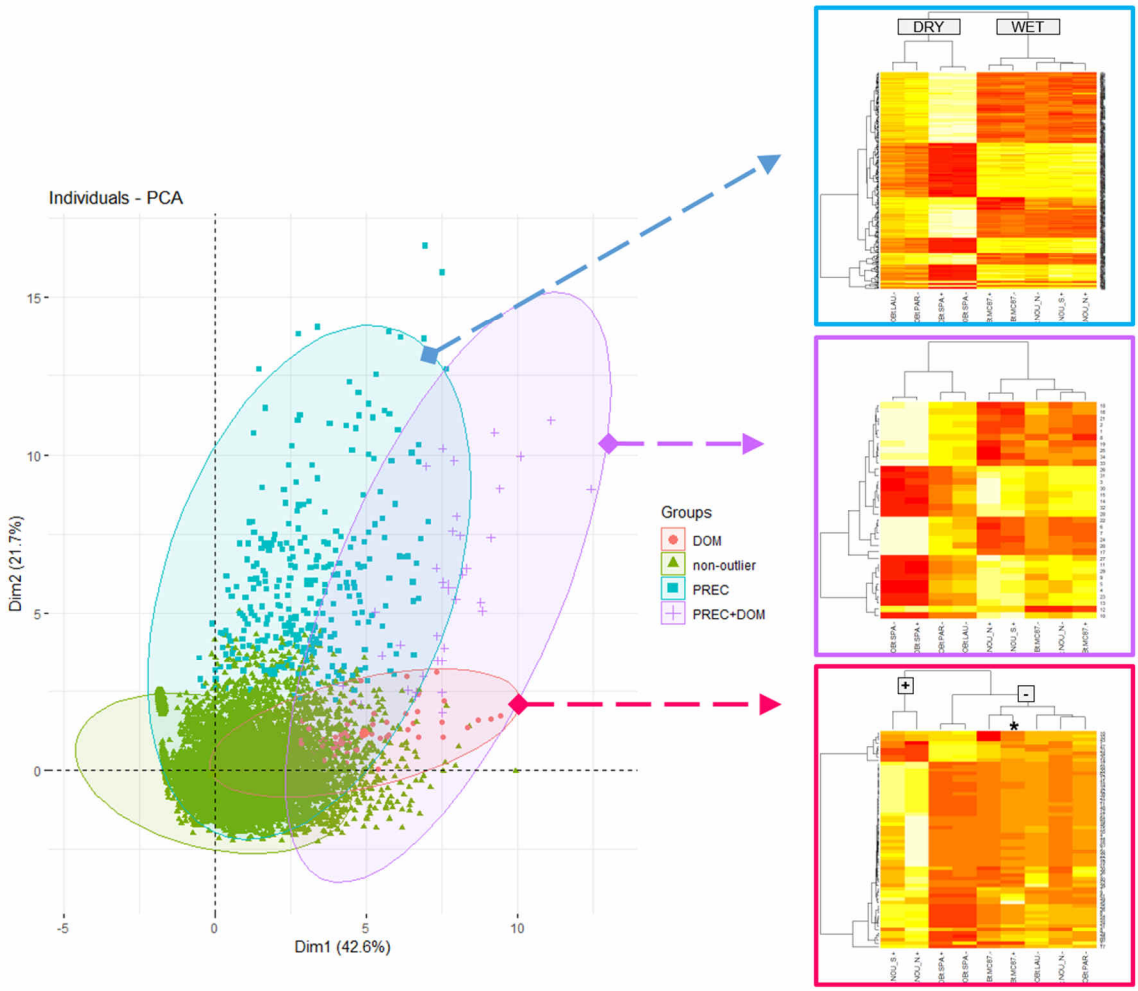
494 to distinguish four groups of SNPs within each species: (i) neutral SNPs, (ii) climate adaptation

495 SNPs showing (clinal) variations in allele frequency in relation to regional precipitation, (iii)

496 domestication SNPs showing differences in allele frequency in relation to local pre-Columbian

497 occupation, and (iv) climate and domestication SNPs showing allele frequency variations in

498 relation to both, **Figure 7**.



499

500 **Figure 7.** Principal Component Analysis representing the multivariate projection of SNPs
501 based on SNP-specific estimates of XtX_i, δ_i, Δ_i and $\Delta_{i,s}$ in *Oenocarpus bataua*. Green: neutral
502 SNPs (*i.e.* non-outlier); blue: climate adaptation SNPs ("PREC") ; pink: domestication SNPs
503 ("DOM") ; violin: climate and domestication SNPs ("PREC+DOM"). Heatmaps on the right
504 show standardized allele frequencies in the different populations and for the different SNPs of
505 each group.

506 **Discussion**

507

508 This study opens a new research framework to document microevolution in non-model
509 Amazonian palms. We provide original observational genomic data describing the state and
510 distribution of genomic diversity in French Guiana, and we bring new knowledge about the
511 microevolutionary processes at play, disentangling neutral and selective processes on one side,
512 and natural and human-mediated ones on the other.

513 First of all, we must recall that all the four species were not present in all study sites and local
514 conditions of pre-Columbian occupation. This was particularly the case for *Oenocarpus* spp.
515 that were more difficult to find and to collect in natural forest areas than on ring ditches were
516 these species are frequent. As a result, we did not collect any *Oenocarpus* spp. in NOU_S –,
517 while *O. bacaba* was also absent from NOU_N – and MC87 (+ and –). This is consistent with
518 previous observations at the community level by Odonne et al. 2019 who reported an over-
519 abundance of palms in sites with strong evidence of pre-Columbian occupation compared to
520 natural forest landscapes. This constrained our study, as we had to deal with incomplete
521 sampling designs. Nevertheless, the amount of population-scale NGS data acquired was largely
522 sufficient to explore microevolutionary processes in the studied palm species, and to
523 disentangle natural and human mediated ones.

524

525 **Neutral microevolution driven by gene flow and admixture.**

526 Patterns of genome-wide diversity revealed a west-east genetic structuring at the regional scale,
527 with similar trends between the four species. Genome-wide structure and differentiation are
528 commonly driven by neutral evolutionary processes, in particular gene flow. This is comforted
529 by significant isolation by distance we detected in three species, indicating that regional patterns
530 of genomic diversity are primarily driven by gene flow, which gradually decreases with the

531 geographic distances between populations. We also detected intriguing patterns of genome-
532 wide genetic structure in *Astrocaryum* spp. in the study site of MC87. In particular, the natural
533 population (–) of *A. paramaca* revealed high levels of differentiation (about 40%) with
534 populations from other study sites, while the population on the ring ditch was closer to
535 populations from other study sites than to the population in the surrounding natural forest. A
536 similar pattern was also observed in the congeneric species *A. sciophilum*, although to a lesser
537 extent, suggesting a site-specific process probably involving inter-specific hybridization. This
538 hypothesis was corroborated by admixture tests, which suggested inter-specific admixture
539 between *A. paramaca* and *A. sciophilum* in the study site of MC87. Similarly, the genetic
540 structure of *Oenocarpus bataua* revealed a site-specific structure in SPA+ corroborated by
541 admixture tests suggesting inter-specific hybridization between *O. bacaba* and *O. bataua*.
542 These site-specific patterns of inter-specific hybridization were neither expected nor anticipated
543 when designing this study and carrying out the sampling. Most interestingly, *Astrocaryum*
544 putative inter-specific hybrids were identified either as *A. paramaca* or as *A. sciophilum*,
545 suggesting that they alternatively exhibit the morphological characteristics of one or the other
546 species. The two putative *Oenocarpus* hybrids, on their side, were both identified as
547 *Oenocarpus bacaba*. While there is no other species of *Oenocarpus* known in French Guiana,
548 there is at least fifteen different species of *Astrocaryum* recorded on *GBIF* (GBIF Secretariat:
549 GBIF Backbone Taxonomy. https://doi.org/10.15468/39omei Accessed via
550 https://www.gbif.org/species/2738048 [30 March 2022]), raising the possibility of complex
551 inter-specific hybridization with possible cryptic species. Even though we cannot conclude
552 about the exact species involved in the pattern observed here, this preliminary observation
553 would deserve in-depth investigation of inter-specific hybridization and introgression in the
554 *Astrocaryum* complex.

555 Independently from site-specific hybridization patterns, estimates of intra-population genetic
556 diversity revealed high heterozygosity (H_o) and significantly negative F_{is}, indicating the
557 absence of inbreeding. These estimates are in line with previous knowledge about the breeding
558 system in Arecoideae that are known to be monoecious and predominantly outcrossed due to
559 protandry and/or genetic incompatibility (Henderson 1986; Eguiarte et al. 1992; Consiglio and
560 Bourne 2001; Picanço-Rodrigues et al. 2015; Gaiotto et al. 2003; Ottewell et al. 2012). The
561 genetic structure and diversity of populations on ring ditches was further close to populations
562 in the surrounding natural forests, indicating the absence of pre-Columbian impacts on
563 population genome-wide diversity and divergence. This result is not surprising, considering the
564 geographic proximity between "+" and "–" populations within study sites, which are probably
565 connected by extensive gene flow. The absence of genome-wide differentiation, however, does
566 not preclude the existence of SNP-specific selective processes driven by adaptation and/or
567 domestication.
568
569 **Climate adaptation and pre-Columbian domestication.**
570 Adaptation and domestication are acknowledged as important drivers of microevolution
571 worldwide, but they have been poorly documented in lowland Amazonia. While Central and
572 South America are known to be important centers of plant domestication, most studies have
573 focused on major crops such as maize (Kistler et al. 2018), papaya (Chávez-Pesqueira and
574 Núñez-Farfán 2017), manioc (Mühlen et al. 2019; Rival and McKey 2008; Alves-Pereira et al.
575 2020) or common bean (Rendón-Anaya et al. 2017), which provide the most obvious cases of
576 domestication. On the opposite, studies on minor crops are scarce although they are receiving
577 increasing attention since the last ten years (*e.g.* Brazil nut, Shepard and Ramirez 2011 ; piquiá,
578 Alves et al. 2016 ; peach palm, Clement et al. 2017 ; treegourd, Moreira et al. 2017). For its
579 part, the lack of interest in adaptation can be explained by the popularity of the neutral theory

580 under which the distribution of alleles within species (Kimura 1983) or species within
581 communities (Hubbell 2001) is assumed to be independent from fitness differences between
582 genotypes or species, being thus driven by stochastic mutation, demography and dispersal. In
583 hyperdiverse tropical rainforests, neutral models are powerful to predict global patterns of
584 diversity, as illustrated in the above section, and very useful to overcome the complexity of
585 niche differentiation modelling. Neutral and niche models are however highly complementary
586 (Chave 2004), and the neutral theory provides an elegant neutral hypothesis to test for niche
587 differentiation and adaptation (Leigh 2007). This is precisely the theoretical assumption of most
588 population genetics selection tests, which allows detecting gene- or SNP-specific departures
589 from the genome-wide, supposedly neutral, background of diversity and differentiation
590 (Beaumont and Nichols 1996).
591 By detecting many over-differentiated SNPs in relation to precipitation and pre-Colombian
592 occupation, our results bring new evidence of the coaction of climate adaptation and ancient
593 domestication in shaping patterns of genomic diversity across multiple spatial scales. As
594 expected, divergent selection related to adaptation and domestication affected a very small
595 fraction of the studied SNPs (always below 1.5%). Both the proportion of SNPs and the extent
596 of differentiation (XtX_i) were in the same order of magnitude between climate adaptation and
597 domestication SNPs, in spite of the different geographical scales involved (*i.e.* hundreds of
598 kilometers between study sites with different rainfall *versus* hundreds of meters between local
599 populations in contrasting conditions of pre-Columbian occupation). Regarding climate
600 adaptation, the present results are in line with a previous study in the hyperdominant tree *Eperua*
601 *falcata* which provided another evidence of climate adaptation along the sharp rainfall gradient
602 in coastal French Guiana (Brousseau et al. 2021).
603 Climate and domestication SNPs were located within or in the neighborhood (< 200bp) of many
604 genes whose exhaustive list is provided in **Supplementary material 7**. Although documenting

605 the functions of these genes in *Astrocaryum* spp. and *Oenocarpus* spp. is beyond the scope of
606 this study, we can nevertheless pick a few examples to illustrate the variety of genes involved.
607 For example, we detected climate adaptation SNPs in several genes of major importance for
608 plant development and response to stresses, including ABC transporters (Yazaki 2006; Do et
609 al. 2018), leaf rust disease resistance loci (Lim et al. 2015), Apetala2-like ethylene responsive
610 transcription factor (Licausi et al. 2013), aquaporins (G. Li et al. 2014; Maurel et al. 2015), and
611 several peroxidases (Blokhina et al. 2003; Yoshida et al. 2003). Several domestication SNPs
612 were detected in genes involved in lipid and sugar metabolism that could be of importance for
613 fruit development, including phospholipase D (Sun et al. 2011; Mao et al. 2007; Pinhero et al.
614 2003), acyl-transferases, fructose-bisphosphate aldolase (Feng et al. 2020; Yin et al. 2012),
615 phospholipid-transporting ATPases, and UDP-glucose 6-dehydrogenase 4.
616 Interestingly, many SNPs showed patterns of differentiation in relation to both climate
617 adaptation and domestication, indicating that these two processes are closely intertwined. In
618 other words, pre-Columbian societies had either domesticated "*in situ*" locally pre-adapted
619 populations or had to deal with adaptation during domestication. The absence of genome-wide
620 differentiation between palm populations on ring ditches and surrounding natural populations
621 tend to suggest that palm populations were collected in the forest near to the ring ditches.
622 Moreover, extensive gene flow between wild and domesticated populations had probably
623 continuously homogenized populations, thus preventing the genome-wide differentiation and
624 the fixation of the so-called "domestication syndrome" in domesticated populations (see next
625 section). Instead, SNP-specific patterns of domestication observed here provide a new evidence
626 of the subtle influence of pre-Columbian societies and depicts what is commonly referred to as
627 "incipient" domestication (Lins Neto et al. 2014; Casas et al. 2016; Clement 1999). Gene flow
628 since land abandonment may also have partly erased patterns of differentiation caused by
629 domestication (*i.e.* de-domestication, Qiu et al. 2017). Moreover, many SNPs were detected in

630 one study site only, supporting that pre-Columbian impacts were partly site-specific.
631 Nevertheless, many SNPs were also detected in more than one study site, indicating some
632 common trends in the different study sites, probably caused by similar management practices.
633 Whether observed domestication patterns result from "conscious" domestication through direct
634 selection for desired traits or "unconscious" domestication through indirect local adaptation to
635 anthropogenic landscapes (Gepts 2010; Engelbrecht 1916; Darlington 1973) cannot however
636 be solved yet, and would require in-depth investigation at the phenotypic level to assess which
637 traits have been selected for or against in palm populations established on ring ditches.
638
639 **Moving beyond the domestication syndrome paradigm.**
640 The domestication of plants is a long-term process, with multiple possible outcomes. However,
641 most studies have focused on major crops exhibiting clear phenotypic differences with wild
642 populations, often underpinned by a sharp – genome-wide – genetic differentiation. Studies on
643 major crops led to the elaboration of an earlier model of domestication through which the
644 domestication is initiated by the isolation of a small population with reduced diversity.
645 Domesticated populations are then expected to accumulate phenotypic differences from their
646 wild ancestors under the action of strong selection (*i.e.* artificial selection for desired traits and
647 natural selection exerted by new environmental conditions) reinforced by inbreeding, both
648 resulting in the fast decrease in genetic diversity and in the fixation of phenotypic differences
649 in domesticated populations: the so-called "domestication syndrome" (Hammer 1984; Harlan
650 et al. 1973; Allaby 2014). The domestication syndrome has been extensively documented, and
651 quite over-emphasized (Kantar et al. 2017), leading to a narrow view of the domestication
652 process and to a misleading dichotomous distinction between domesticated varieties with a
653 clear domestication syndrome, and other (supposedly wild) populations. The domestication
654 process is, however, gradual through time and variable across populations (Meyer et al. 2012;
655 O. Smith et al. 2019; Kantar et al. 2017), and it is not necessarily expected to result in a sharp

– genome-wide – differentiation, in particular in cases of domestication "*in situ*" with extensive and continuous gene flow with wild populations (Meyer and Purugganan 2013). In a broader sense, the domestication process is better depicted as the modification of the evolutionary trajectory of a population through human-mediated evolutionary processes (including human-mediated dispersal, artificial selection for useful traits and/or indirect adaptation to anthropogenic landscapes) that can outcome – in most extreme cases – in the fixation of the domestication syndrome.

Because lowland Amazonia offers a great diversity of domestication histories and cases, from "incipiently-" or "semi-" domesticated populations to stable varieties (Lins Neto et al. 2014; Clement 1999), it offers an ideal study system to reconsider the domestication process beyond the domestication syndrome paradigm. Integrating the diversity of evolutionary histories underlying domestication further opens a new perspective toward a better understanding of microevolution in Amazonia, and the present study argues in favor of a paradigm shift to better integrate "incipiently-" and "semi-" domesticated minor crops in domestication studies.

671 **Supplementary materials**

672 **Supplementary material 1 (S1)**. ARECO5000+ Custom probe kit for targeted capture in
673 Arecoideae.

674 **Supplementary material 2 (S2)**. Molecular methods – library preparation, capture, sequencing
675 and adapters.

676 **Supplementary material 3 (S3).** Sequencing and bioinformatics (405 libraries) –
677 supplementary figures, tables and information.

678 **Supplementary material 4 (S4).** Fastq quality check.

679 **Supplementary material 5 (S5).** List of palm samples retained for genetic analyses.

680 **Supplementary material 6 (S6).** Population genetics – supplementary figures and tables.

681 **Supplementary material 7 (S7).** Genes containing climate adaptation and domestication
682 SNPs.

683

684 **Ethics statement**

685 This study was carried out in compliance with the Nagoya protocol and French regulations on
686 access to genetic resources with no direct commercial purposes. Palm samples were collected
687 for fundamental research following declaration to the French Ministry of the Ecological
688 Transition registered under the Internationally Recognized Certificate of Compliance ref.
689 ABSCH-IRCC-FR-245923-1 of 23 May 2018. The authors declare no commercial use of the
690 data generated and that no monetary benefit was derived from this study. Genomic data are
691 made available according to shared values and principles for Open Science.

692

693 **Data and codes availability**

694 Sequencing data (i.e. paired-end reads) are available on the European Nucleotide Archive under
695 accession PRJEB51800. Bioinformatics codes are available on GitLab under Project ID

696 34990830 (https://gitlab.com/LouiseBrousseau/palm-capture-bioinformatics). Data and code
697 remains under embargo until formal acceptance of the present article.
698
699 **Competing interests**
700 The authors declared no conflict of interest.
701
702 **Authors contribution**
703 LB and GO imagined the study and carried out palm sampling. LB designed the capture kit,
704 implemented the bioinformatics pipeline, and carried out bioinformatics and population
705 genetics. SS and AW carried out the molecular experiments (gDNA extraction and purification,
706 library preparation, targeted capture and sequencing of *O. bataua* librairies). All authors wrote
707 and approved the article.
708
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