


# Long-term influence of early human occupations on current forests of the Guiana Shield

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*Abstract.* To decipher the long-term influences of pre-Columbian land occupations on contemporary forest structure, diversity, and functioning in Amazonia, most of the previous research focused on the alluvial plains of the major rivers of the Amazon basin. Terra firme, that is, nonflooded forests, particularly from the Guiana Shield, are yet to be explored. In this study, we aim to give new insights into the subtle traces of pre-Columbian influences on present-day forests given the archaeological context of terra firme forests of the Guiana Shield. Following archaeological prospects on 13 sites in French Guiana, we carried out forest inventories inside and outside archaeological sites and assessed the potential pre-Columbian use of the sampled tree species using an original ethnobotanical database of the Guiana Shield region. Aboveground biomass (320 and 380 T/ha, respectively), basal area (25–30 and 30–35 m<sup>2</sup>/ha, respectively), and tree density (550 and 700 stem/ha, respectively) were all significantly lower on anthropized plots (As) than on nonanthropized plots (NAs). Ancient human presence shaped the species composition of the sampled forests with *Arecaceae*, *Burseraceae*, and *Lauraceae* significantly more frequent in As and *Annonaceae* and *Lecythidaceae* more frequent in NAs. Although alpha diversity was not different between As and NAs, the presence of pre-Columbian sites enhances significantly the forest beta diversity at the landscape level. Finally, trees with edible fruits are positively associated with pre-Columbian sites, whereas trees used for construction or for their bark are negatively associated with pre-Columbian sites. Half a millennium after their abandonment, former occupied places from the inner Guiana Shield still bear noticeable differences with nonanthropized places. Considering the lack of data concerning archaeology of terra firme Amazonian forests, our results suggest that pre-Columbian influences on the structure (lower current biomass), diversity (higher beta diversity), and composition (linked to the past human tree uses) of current Amazonian forests might be more important than previously thought.

*Key words:* Amazonian forest; archaeology; ethnobotany; Guiana Shield; historical ecology; pre-Columbian settlements; ring-ditched hills.

## INTRODUCTION

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A growing body of archaeological and pedological evidence, accumulated since the 1990s, suggests that Amazonian rainforests might have been much more densely

occupied and intensely modified by Amerindian societies before the First Contact than previously thought (Heckenberger et al. 2003, 2008, Clement et al. 2015). By challenging the common idea of “pristine” tropical forests (Bahuchet et al. 2000, Barlow et al. 2012), these discoveries have stimulated tropical forest scientists to consider pre-Columbian human activities as one of the potential factors shaping the current biodiversity, structure, and functioning of Amazonian rainforests (Clement et al. 2015). Throughout the Amazonian basin, several studies in historical ecology have highlighted the importance of human activities in the composition and structure of modern forests. This long-lasting impact was first detected in the structure and chemistry of soils (Sombroek 1966, Smith 1980, Schmidt and Heckenberger 2009, Arroyo-Kalin 2010, Schmidt 2010) with Anthropogenic Dark Earths (ADE), that is, black, C-, P- and N-enriched, anthropogenic soils called *Terra preta do Índio* in Brazilian Portuguese. Floristic composition has also been directly impacted (Heckenberger et al. 2007, Levis et al. 2012, 2017) with the possible dissemination of many wild or incipiently domesticated species, such as *Bertholletia excelsa*, the Brazil nut tree (Clement 1999, Shepard and Ramirez 2011), and many palms, as well as domesticated crop plants (Balée 2013, McMichael et al. 2015, Piperno et al. 2015). Lastly, Amazonian landscapes, with their entanglements of forests and savannas, also generally reflect the presence of humans with large earthworks detectable from the sky such as geoglyphs (Schaan 2011, Stahl 2015, Watling et al. 2017a, Souza et al. 2018), residential mounds and causeways (Erickson 2000), and cities (Heckenberger et al. 2008). These impacts have mainly been shown for the alluvial plains of the Xingu, the Tapajos, the Madeira, and Acre state. Traces of past human activity are nonetheless numerous in the Guiana Shield area, differing from southern Amazonia by its climate, substrate, and biogeographical history. Archaeological artefacts are frequent from the coastal area to the southern border of the Guiana Shield, and anthropogenic landscapes are still present. On the coastal plains savannas, raised fields are amongst the most amazing structures seen in tropical ecosystems (Rostain 2008, 2010, 2012). It is hypothesized that they originate from abandoned Amerindian fields and subsequently engendered self-organizing processes driven by ecosystem engineers (ants, termites, earthworms, and woody plants) that have preserved the physical vestiges of these fields up to the present day (McKey et al. 2010). Further south, in the forest-covered part of the Guiana Shield, hills topped by ring-ditches or simply crossed by anthropogenic ditches (Mestre et al. 2008, Mestre 2013) can be observed. These structures testify to the major earthworks made by pre-Columbian Amerindians with many sites exceeding several hectares in area. Few data exist about these sites in the Guiana Shield, but a sort of parallel can be made with the geoglyphs observed in the Brazilian state of Acre (Saunaluoma and Schaan 2012, Watling et al.

2017a). But most earthworks of the Guiana Shield are still covered by dense and so-called “mature” forests, whereas Acre structures were observed after deforestation. As highlighted by the recent papers by Levis et al. (2012, 2017) and Watling et al. (2017a), the influence of pre-Columbian occupation on terra firme forest composition and diversity is hotly debated everywhere in Amazonia (Bush et al. 2015, Piperno et al. 2015, 2017, Watling et al. 2017b), tipping in favor of an enrichment of useful species by previous occupants (Junqueira et al. 2011). For the Guiana Shield, the results obtained by Levis et al. (2017) suggest a weak influence of pre-Columbian occupation on forests. However, by focusing only on some edible domesticated species that are widely consumed throughout Amazonia, this study ignores nondomesticated species and those that are consumed in certain regions only. Second, past human influences must have been much more diverse than just the favoring of edibles and large seed trees. Over generations, the falling of trees to build houses or using wood or bark for crafts and medicine might have depleted the surrounding populations of the species so used for a long time. The sparsity of archaeological data available for the interior of the Guiana Shield might also lead to a misunderstanding of the regional situation.

In this paper, we aim to give new insights into the archaeological context of terra firme forests of the Guiana Shield, and to help decipher the subtle traces of pre-Columbian influences on present-day forests. Moreover, the unique context in French Guiana of massive earthworks and “preserved” long-lasting forests (Barthe et al. 2017) might be a perfect combination to improve our understanding of long-term human–forest interactions in Amazonia. Hypothesizing that French Guianese earthworks have probably been subject to long-term occupation, either ceremonial, housing, or public gathering, the vegetation growing on them should have been impacted by a variety of uses, and this may have long-term aftereffects on their present-day structure and composition. Comparing these anthropized areas to areas with no evidence of past human presence in order to test the Levis et al. (2017) hypothesis is a preliminary step. In a second step, we interpret the differences observed assuming that different uses of biodiversity, such as consumption of fruit gathered from the wild and prepared at a residential site, peeling off bark for medicinal purposes, or felling of trees to make house posts, had contrasted impacts on the surrounding vegetation. To reach this objective, a nearly exhaustive historical compilation of ethnobotanical uses in the region was amassed. It concerns five of the Amerindian groups of the Guianas belonging to the three linguistic families represented today in the area: Carib, Arawak, and Tupi-Guarani.

## METHODS

This study involved 13 forest permanent plots, including 12 from the Guyafor (Grau et al. 2017) network

distributed throughout the northern two-thirds of French Guiana (Fig. 1). The Guyafor network has been designed to assess the main climate and geological drivers of the old-growth forests in northern French Guiana. We selected all permanent plots (Table 1, SUPMAT 1, 2, 3) with high-level of botanical determination that respect the international standards (Chave et al. 2019), most of them belonging also to the Guyadiv network (<http://atdnmorphospecies.myspecies.info/node/781>). All individual trees ( $\geq 10$  cm in diameter at breast height) present in the plots were marked, mapped, and measured. Common species were identified in the field, and vouchers collected on all other species were identified and deposited at Herbar IRD de Guyane (CAY). The total data set included 7,820 trees. Individuals determined to the genus level only represent 4.63% of all individuals.

*Archaeological research*

The surface of each plot was surveyed by archaeologists. Evidence for pre-Columbian human occupations (such as artifacts, dark soils, earthworks) was searched

for in the field, by superficial prospection of the ground surface while walking and carefully examining soil heaps expelled from burrows and mounds resulting from unrooted trees. Exploratory test pits were also dug to confirm surface observations and to establish soil profiles. This allowed classifying plots as either anthropized (A) or less- or nonanthropized plot (NA). In fact, site detection in the Guianas can often be accomplished by means of a “simple” pedestrian survey, notably on the Precambrian Shield. A trained eye can spot ceramic shards or lithic debris located between the roots of fallen trees and around holes made by agoutis or armadillos. Charcoals found in anthropized plots were radiocarbon dated after calibration using OxCal ver. 3.10. (Appendix S1). Details (type of occupations, site descriptions, dates) on the As and NAs can be found in supplementary materials (Appendices S2 and S3).

Compared to the coastal zone, the area of high forest on terra firme where the studied plots are located was poorly studied by archaeologists working in the Guiana Shield, because it is isolated and difficult to access. All the plots are within 80 km of modern Amerindian villages. The selected Amerindian groups for the

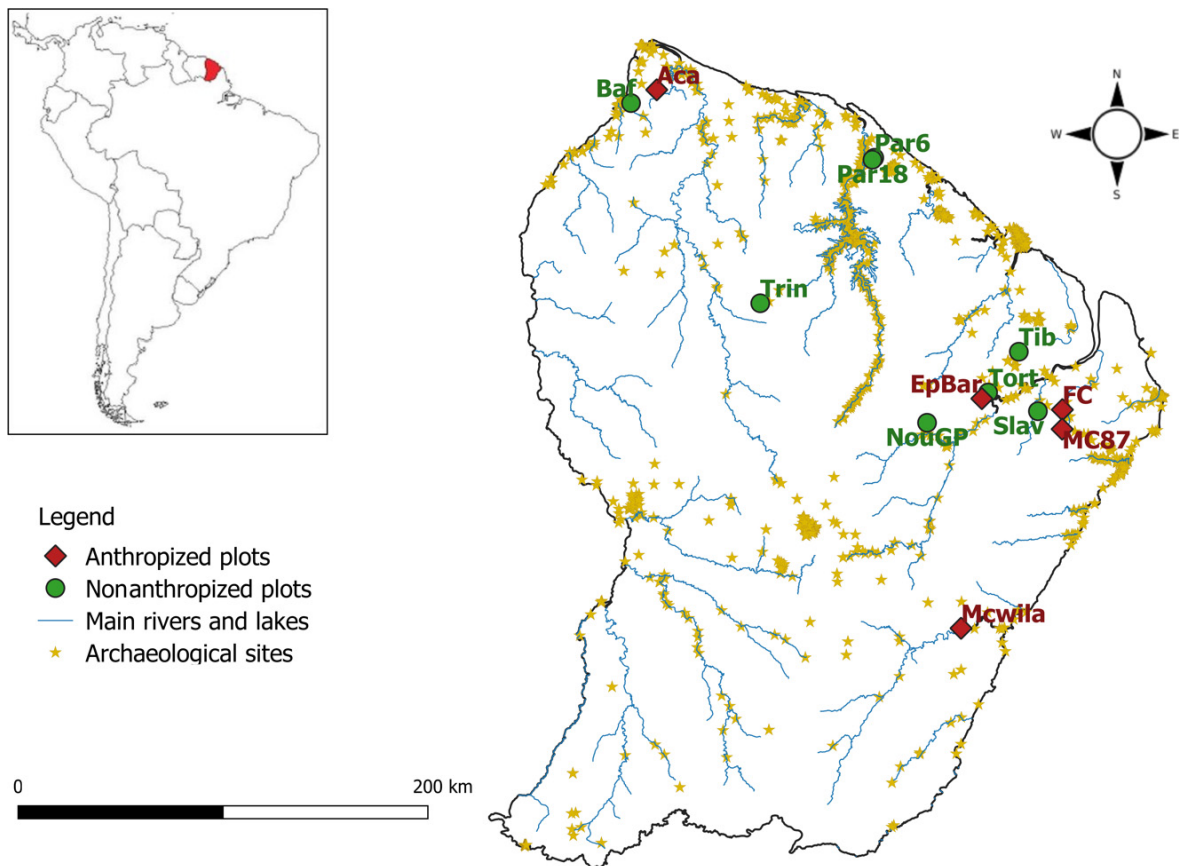


FIG. 1. Overview of the studied area and the anthropized (red diamonds) and nonanthropized (green circles) plots. Main rivers and archeological sites (listed in the Patriarce database of the Direction régionale des affaires culturelles—Service régional d’Archéologie of French Guiana) are reported.

TABLE 1. Overview of the sampled plots in French Guiana, botanical description, plot area, and occupation dates.

Plot name	<i>N</i> trees	<i>N</i> family	<i>N</i> genus	<i>N</i> species	% Determination	Area (ha)	Altitude (m)	Rainfall (mm)	Topography	Soil type	Distance to river (m)	Site type	Dating (AD)
Aca	454	42	93	148	95.59	1.00	45	3300	Hilltop	DVD	2931	A	1100–1600
Baf	756	39	106	183	93.65	1.00	33	3100	Hilltop	DVD/Alt	1411	NA	–
EpBar	415	39	100	164	98.80	0.80	146	4500	Hilltop	DVD	4940	A	1000
FC	515	44	106	194	98.83	1.14	41	4500	Hilltop	DVD	1298	A	700–1400
MC87	821	45	127	274	98.78	1.83	84	4300	Hilltop	DVD	3126	A	400–1300
Mewila	654	41	103	173	98.32	1.17	100	2900	–	–	1362	A	NA
NouGP	536	43	104	169	89.37	1.00	108	3900	Slope	DVD	5175	NA	–
Par18	499	42	103	158	96.39	1.00	31	4100	Slope	SLD	3751	NA	–
Par6	964	41	106	189	94.19	1.56	42	4100	Slope	Alt/SLD/DhS	4756	NA	–
Slav	620	44	106	200	88.23	1.00	87	4500	Hilltop	DVD	2549	NA	–
Tib	440	41	114	176	95.00	1.00	82	5100	Hilltop	DVD/Alt	12346	NA	–
Tort	496	46	122	193	94.15	1.00	170	4500	Hilltop	DVD	4012	NA	–
Trin	650	40	112	187	98.92	1.00	146	3500	Hilltop	DVD	8996	NA	–

Note: Soil type was associated to drainage conditions following Sabatier et al. (1997): deep vertical drainage (DVD), vertical drainage until 100-cm depth (Alt), superficial lateral drainage (SLD), and hydromorphic downhill system (DhS).

ethnobotanical study are distributed in all habitats, and used to forage in all forest types. Although most of the present archaeological knowledge originates from discrete reports, about 1,300 geolocated references, including archaeological sites as much as single objects, were recorded in the database of the French Guiana archaeological service (Fig. 1). The studied archaeological sites yielded stone and ceramic material, but little can be said about cultural affiliation, even compared to the coastal zone. We might, however, discern various sites such as (1) open-air sites with brown soils and few material (Aca) and (2) ditched sites with (a) either a short ditch closing a hillock (*EpBa*) or (b) encircling a hilltop (*MC87*, *FC*, and *MCwila*). This second type of site may have brown and dark-colored soils. Sites are generally situated on hilltops and usually are restricted to the summit of a hillock or restricted to a part of a plateau.

#### *Effect of past anthropization on current tree communities*

The effect of past anthropization was first investigated on standard forest structure descriptors: tree density, quadratic diameter, basal area and aboveground biomass calculated with the BIOMASS package (Réjou-Méchain et al. 2017). Differences between As and NAs were assessed with Wilcoxon–Mann–Whitney nonparametric tests.

Botanical composition among plots was first compared with a detrended correspondence factor analysis (DCA) under vegan R package (Oksanen et al. 2015). Then, any past anthropization effect on the 20 most abundant families was tested with Wilcoxon–Mann–Whitney test. Finally, we looked for indicator species, keeping in mind that correlation can be either direct (managed species) or indirect (consequence of a specific pattern of recolonization after occupation), and positive (species for which human occupation is favorable) or

negative (species for which past human occupation is detrimental). We used the Dufrêne and Legendre (1997) methodology implemented with the package *indicpecies* (De Caceres et al. 2012).

Functional composition was also assessed to avoid local botanical variations in tree assemblages that are of little importance for forest functioning (Héroult and Piponiot 2018). The four chosen functional traits represent key dimensions of the tree functional strategy response to disturbance (Héroult et al. 2010, Flores et al. 2014, Hogan et al. 2018): wood density, seed mass, specific leaf area, and maximum diameter from a regional trait database (Baraloto et al. 2010a, Héroult et al. 2011). The community weighted means of these functional traits were calculated. Differences between As and NAs were assessed with Wilcoxon–Mann–Whitney nonparametric tests.

Neutral and functional Shannon alpha and beta diversities were calculated for each plot using the “entropart” package (Marcon and Herault 2015a, b). (1) For alpha diversity, we used the function `AlphaDiversity()` that calculates the reduced-bias total alpha diversity of each community without (neutral diversity) and with a functional tree (functional diversity). The functional tree was obtained using the following procedure (Héroult 2007, Héroult and Honnay 2007). First, a similarity matrix between species was calculated based on the four chosen (see above) functional traits and using Gower’s similarity coefficient, and the resulting matrix was used to cluster the species using Ward’s method. The resulting cluster was then used in the `AlphaDiversity()` function. Differences in neutral and functional Shannon alpha between As and NAs were tested using Wilcoxon–Mann–Whitney tests. (2) We assessed beta diversity using the following procedure. From the 13 investigated sites, we randomly sampled assemblages of four sites and calculated (1) their beta diversity and (2) the



proportion of anthropized plots in the assemblages (0, 25, 50, 75, or 100%). We repeated the procedure 200 times per proportion of anthropized plots. Then, we compared beta-diversity levels between the different proportion of anthropized plots and tested the hypothesis that the presence of anthropized forests in the landscape increases the overall beta diversity with a Spearman's rank correlation test.

### *Ethnobotanical analyses*

*Data collection.*—Because of the absence of an existing database on the uses of plants in forests of the Guiana Shield, a compilation of contemporary ethnobotanical surveys was conducted. First, species represented by only one or two individuals (6.6% of all individuals) were excluded, considering that rare species are less known and therefore more likely to be misidentified. A comprehensive ethnobotanical database was then created considering the available information of the 457 remaining species present in all sampled plots.

Although contemporary uses probably differ in some ways from past uses, the compilation of available information for present-day Amerindian groups (Palikur, Arawak, Wayãpi, Teko, and Kali'na) belonging to the three linguistic families in French Guiana (Arawak, Tupi-Guarani, and Karib) was thought to be the best proxy for potential pre-Columbian uses. The choice of the data sets to be compiled was driven by three selection criteria: (1) geographical coherence (inclusion of the main cultural groups of the Guiana Shield and their knowledge of tree species in the region), (2) completeness (high number of taxa recorded), and (3) quality (reliable methodologies). Most of the information is comprised of unpublished or sparsely published data from previous works, with the exception of those available for the Arawak and Kali'na ethnic groups.

All the ethnobotanical data were obtained before adoption of the ABS laws in French Guiana, and no written informed consent document was signed between traditional authorities and the researchers, except for the Teko, with whom a document was signed between the Chief and the concerned investigators in July 2013. The other works were concluded under the verbal agreement of authorities during long years of continuous fieldwork.

Palikur and Arawak belong to the Arawak linguistic family, Wayãpi and Teko to the Tupi-Guarani linguistic family, and Kali'na to the Karib linguistic family. These three families are among the most important of those spoken in the Eastern Amazonian lowlands. Five Amerindian groups now occupy different ecosystems, ranging from estuaries and coastal savannahs to terra firme forests in French Guiana. Data were obtained as follows:

- Palikur ethnobotanical data were accumulated during 34 yr (1972–2012) of research with a dozen key knowledge holders of Palikur communities from French Guiana. The knowledge was recorded during several

research projects associating Palikur collaborators, through ethnobotanical walks and plot inventories, around Saint-Georges de l'Oyapock and Regina villages. Some published works include Grenand et al. (2004) and Ogeron et al. (2018).

- Wayãpi ethnobotanical data were collected over 38 yr of research with some 20 key knowledge holders of Wayãpi communities of French Guiana. The knowledge was recorded through several research projects associating Wayãpi collaborators. Methods used were ethnobotanical walks and plot inventories, around Trois-Sauts and Camopi villages. Some published works include Grenand (1980) and Grenand et al. (2004).
- Kali'na ethnobotanical data were compiled integrating bibliographic data (Aublet 1775, Ahlbrinck 1931, Kloos 1971, van Andel 2000, ONF, 2004) and field data (ethnobotanical studies conducted between 2006 and 2008). The only field data were recorded during a 2-yr-long research program, mainly based on ethnobotanical walks with four collaborators around Awala-Yalimapo village, and restituted to the Kali'na in 2008.
- Teko ethnobotanical data were recorded from 2013 to 2015 through ethnobotanical walks and repeated passages in the sampled plots, located around Camopi village, with seven informants.
- Arawak ethnobotanical bibliographical data were obtained from Arawak populations in northwestern Guyana (van Andel 2000). According to the author, they were completed through repeated passages in seven plots of one hectare and through ethnobotanical walks.

*Traditional uses.*—Traditional use categories were compiled following the methodology developed in previous studies (Prance et al. 1987, Grenand 1992, Balée 1994, Chazdon and Coe 1999): “construction,” “firewood,” “human food,” “medicine and magic,” and “arts and crafts.” A species can enter from zero to five categories. The “construction” category includes species used for posts and other structural elements of buildings. Species of large diameter (>50-cm diameter at breast height) used now as timber in the Guiana Shield (Fargeon et al. 2016, Pioniot et al. 2018, 2019) and requiring the use of a chainsaw, were removed. Without metal, these species were significantly less used by pre-Columbian populations than in the present day. Species requiring no mechanical process for preparation of their wood (round wood) were retained for analysis. The “firewood” category was intentionally kept apart from construction woods, as contemporary Amerindians often collect firewood dry, leading to a distinct pattern of collecting. The “human food” category encompasses main and secondary foods, as well as plants used for seasoning, excluding plants used as fishing/hunting baits. The “medicinal and magic” category includes medicinal plants, poisons, body dyes, and plants used for hygiene.

The category “arts and crafts” includes plants used to make musical instruments, weapons, games, tools, paddles, pirogues, and artisanal dyes.

**Plant parts.**—The second system of classification used is that of the “plant parts” categories, as the use categories are not necessarily the best proxy to determine the impacts of traditional uses on the resource (felling of a tree to make a house has evident consequences, but taking a piece of bark from a tree for medicine might provoke a defensive reaction paradoxically increasing the tree’s probability of survival). We judged that making categories of both uses and parts at the same time would split the data set into too many subtle categories. Plant parts categories we retained are “bark,” “wood and stems,” “seeds and fruits,” “leaves and flowers,” “exudates,” and “underground organs.”

#### Statistical analyses

Synthetic use values were established separately for traditional uses and for plant parts, in a binary way, based on the assumption that although contemporary uses may reflect past uses, the frequency of contemporary use does not necessarily reflect the frequency of pre-Columbian use. Each species cited at least once for a given contemporary use was thus given a use value of 1 for the corresponding category (traditional uses or plant parts), regardless of how many present-day groups use it. The major advantage of the nonquantitative approach is to avoid the bias induced by the variable presence of a species in the territories of different ethnic groups within the region, and the methodological

differences among the ethnobotanical studies, leading to imbalances between cultural groups.

To compare the distribution of use values and plant parts (both expressed as a % of individual trees that may be used in a given plot) between As and NAs, Wilcoxon–Mann–Whitney tests were used.

## RESULTS

### Forest structure, composition and diversity

Forest structure was significantly different between As and NAs (Fig. 2). While As had a median aboveground biomass of about 320 T/ha, the aboveground biomass of the NAs control plots was 380 T/ha on average. The same applied for basal area and tree density with, respectively, 25–30 m<sup>2</sup>/ha and less than 550 stem/ha for As and 30–35 m<sup>2</sup>/ha and up to 750 stem/ha in NAs. Quadratic diameter only was similar, around 28 cm, in As and NAs.

The forest composition of As, as assessed with the DCA, was very well separated from NA along the first axis (Fig. 3) that represents 35% of the observed variation in species composition. Past human occupation is the main source of differences in species composition among our sampled plots and this is reflected in the detailed analysis of the 20 most abundant families that were unequally distributed between As and NAs (Appendix S4: Fig. S1; Appendix S5: Table S1). Five families had clear patterns of segregation ( $P < 0.05$ ). These are Arecaceae (e.g., *Astrocaryum sciophyllum*, *Oenocarpus bacaba*), Burseraceae, and Lauraceae, which are significantly more frequent in As; and Annonaceae

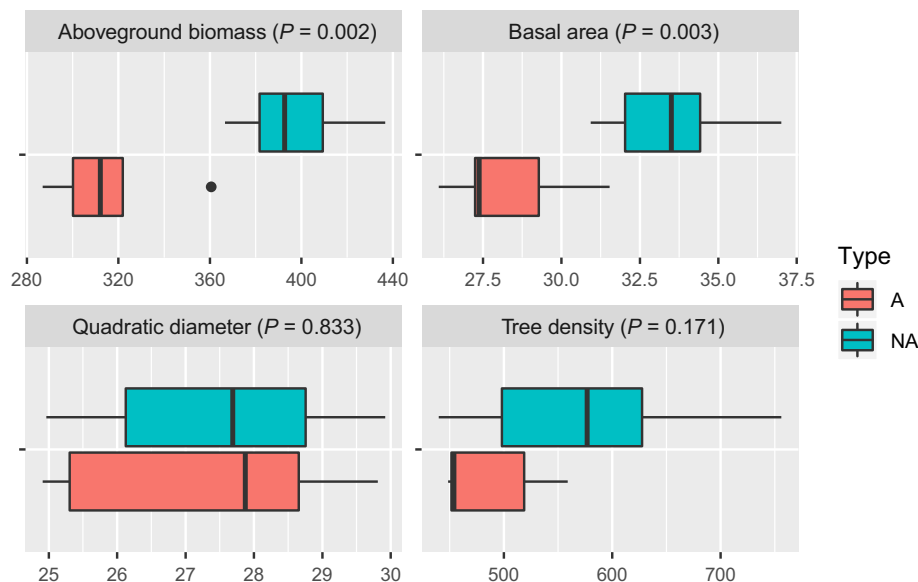


FIG. 2. Comparison of forest structure descriptors (aboveground biomass in T/ha, basal area in m<sup>2</sup>/ha, quadratic diameter in cm and tree density in stem/ha) between anthropized (A) and nonanthropized (NA) plots.  $P$  values from Mann–Whitney nonparametric tests.

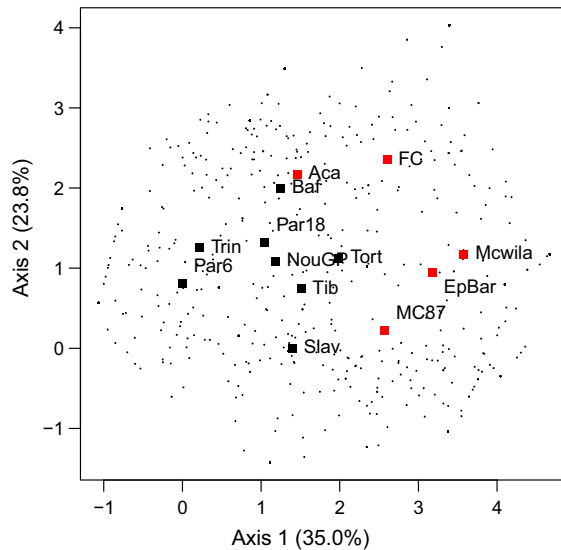


FIG. 3. Anthropization is the main factor driving the forest community composition. Detrended correspondence analysis with species as small dots and large dots as sampled sites, either As (black) or NAs (red).

and Lecythydaceae (e.g., *Couratari multiflora*, *Lecythis persistens*), which are associated with NAs.

Among the four investigated functional traits (Fig. 4), tree height only was significantly different, although marginally, between As (32.5 m on average) and NAs (33.5 m). However, even if not significant, seed mass and wood density were lower in As than in NAs, and

SLA averaged 31–32 cm<sup>2</sup>/g in As and less than 30 cm<sup>2</sup>/g in NAs.

Both neutral and functional alpha diversities did not differ between anthropized (A) and nonanthropized (NA) plots (Appendix S6; Fig. S1), even if the functional diversity tended to be higher in A plots. Regarding beta diversity, (1) the value of the neutral beta diversity significantly increased with the proportion of anthropized (A) plots in the simulated assemblages (Spearman's rank correlation test,  $r = 0.31$ ,  $P < 0.001$ ) but saturated for proportions above 50% (Fig. 5); and (2) the value of the functional beta diversity showed no significant trend (Spearman's rank correlation test,  $\rho = -0.06$ ,  $P > 0.05$ ), but a hump-shaped pattern with the proportion of anthropized (A) plots in the simulated assemblages (Fig. 5).

#### Ethnobotanical results

On average, among the different species, 47.7% (218/457) are used for crafts, 32.8% (150/457) as building material, 27.8% (127/457) for medicinal/magical use, 27.6% (126/457) are used as firewood, and 26.7% (122) produce plant parts edible for human food. Considering the parts used, the most frequent use is of the wood (58.9%; 269/457). Seeds and/or fruits are used for 30.6% of the species (140/457), bark for 25.2% (115/457), exudates for 10.3% (47/457), leaves and/or flowers for 6.8% (31/457), and roots or other underground parts for 0.9% (4/457).

Trees used as human food were significantly more abundant ( $P = 0.03$ ) in As than in NAs (Fig. 6). No conclusion can be drawn for species in the “firewood,”

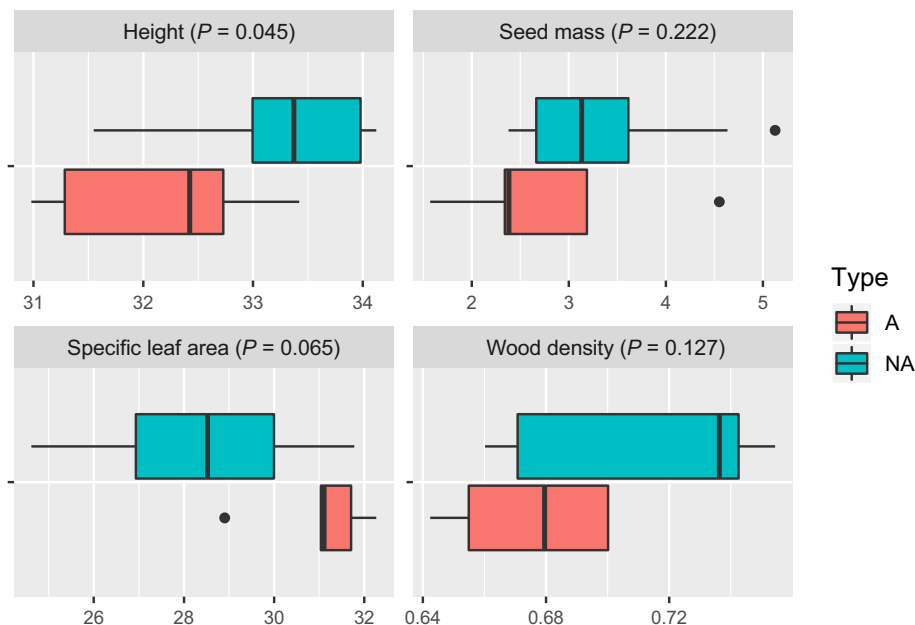


FIG. 4. Comparison of functional trait community weighted means (height in m, seed mass in g, specific leaf area in cm<sup>2</sup>/g, and wood density in g/cm<sup>3</sup>) between anthropized (A) and nonanthropized (NA) plots.  $P$  values from Mann–Whitney nonparametric tests.

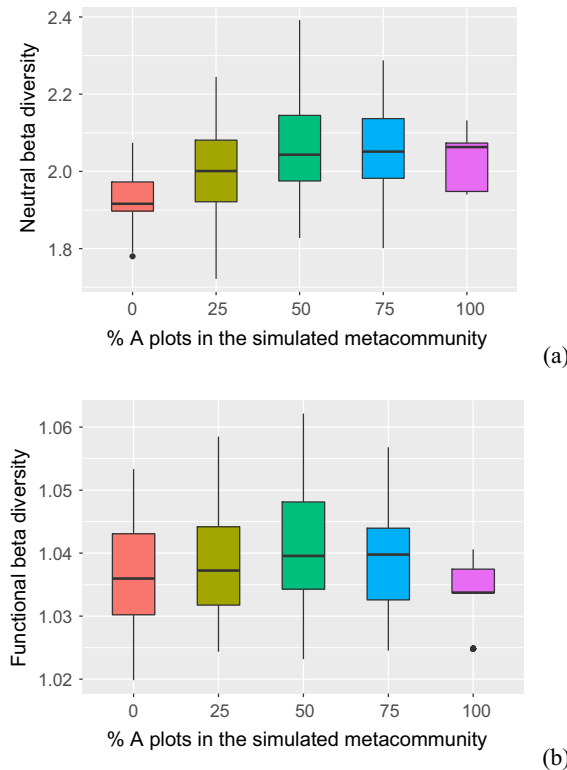


FIG. 5. Comparison of neutral (a) and functional (b) beta-diversity levels between different proportion of anthropized plots in randomly sampled plot assemblages.

“medicine and magic,” and “arts and crafts” categories, owing to their high  $P$  values. Last, species used in construction are more often present ( $P = 0.045$ ) in nonanthropized plots than in As.

Plants with useful seeds and fruits ( $P = 0.045$ ), exudates ( $P = 0.171$ ), leaves and flowers ( $P = 0.171$ ), and underground organs ( $P = 0.241$ ) were, at diverse scales, more abundant on As than on NAs (Fig. 7). The most striking difference concerned species with useful seeds and fruits. Conversely, an increase in the abundance of plants used for their bark ( $P = 0.045$ ) was observed for the NAs, whereas no trend can be determined for the species used for their wood and stems ( $P = 0.435$ ), but the variation in the proportion of trees used for wood among NA plots seems higher than among A plots.

## DISCUSSION

In this paper, we aimed to help decipher the subtle traces of pre-Columbian influences on the structure, diversity, and composition of tree communities in present-day forests of the Guiana Shield. We found that (1) above-ground biomass, basal area, and tree density were all significantly lower on pre-Columbian sites; (2) pre-Columbian presence shaped the current variation in species composition with 5 among the 20 most abundant

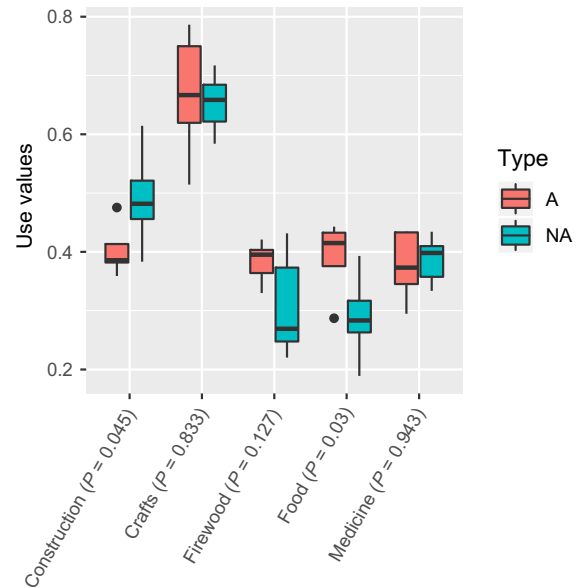


FIG. 6. Comparison of use values (% of trees per plot that can be used for a given use) between anthropized (A) and nonanthropized (NA) plots.  $P$  values from Mann–Whitney non-parametric tests.

families displaying a clear pattern of segregation (Arecaceae, Burseraceae, and Lauraceae associated to pre-Columbian presence and Annonaceae and Lecythidaceae associated to pre-Columbian absence); (3) the presence of pre-Columbian sites strongly enhances the forest beta diversity at the landscape level; and (4) on pre-Columbian sites trees with edible fruits are more frequent and trees used for construction are less frequent.

### *Forest structure—a lower biomass and tree density on pre-Columbian sites*

A major outcome of this study is that the overall forest structure on pre-Columbian sites is still different from undisturbed forests: a lower above-ground biomass, basal area, and a lower tree density per hectare. Given that our sampled plots were disturbed a long time ago, at least five centuries, this lasting signature of pre-Columbian occupations on the current forest biomass is remarkable. A first hypothesis lies in a very slow recovery of the forest after disturbance by pre-Columbian occupations. From ongoing research, we do know that (1) gently disturbed Amazonian forests (losses of 10–50% of the initial system biomass) are expected to recover their predisturbance biomass and structure in less than a century (Blanc et al. 2009, Rutishauser et al. 2015, Piloniot et al. 2016, Hiltner et al. 2018) and that (2) secondary forests (losses of 100% of the initial system biomass) took a median time of 66 yr to recover to 90% of old-growth values in the neotropics (Poorter et al. 2016). This long-recovery-time first hypothesis is thus very doubtful. A possible alternative hypothesis lies in



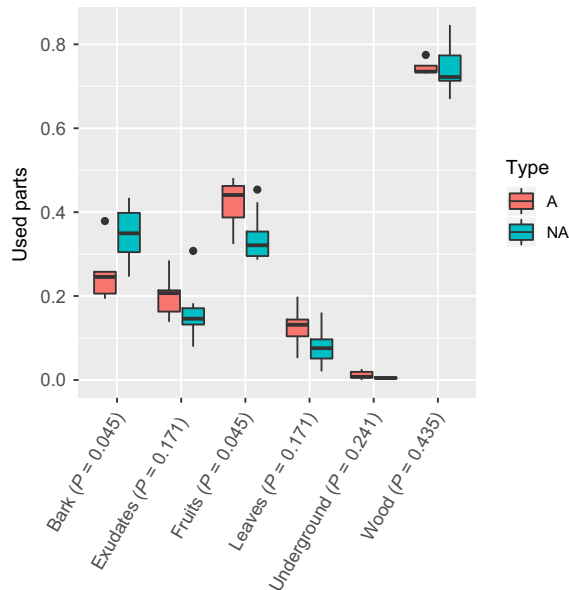


FIG. 7. Comparison of used parts (% of trees per plot for which a given part can be used) between anthropized (A) and nonanthropized (NA) plots.  $P$  values from Mann–Whitney non-parametric tests.

changes in soil fertility. We do know that (1) pre-Columbian occupancy generally increases the overall soil fertility (Quintero-Vallejo et al. 2015) and that the overall soil fertility directly influences forest structure and dynamics, accelerating tree turnover rates and ultimately diminishing the forest biomass (Quesada et al. 2012). This hypothesis is confirmed by the functional analyses where pre-Columbian sites have more acquisitive tree ecological strategies (lower wood density, lower seed mass, higher specific leaf area, and lower maximal stature; Fig. 4), typical of high-resource-levels environment (Baraloto et al. 2010b, 2012, Sterck et al. 2011). Conversely, nonoccupied plots are dominated by conservative ecological strategies (high wood density, seed mass, maximal stature, and low specific leaf area). A self-maintaining high forest dynamic level mediated by the modified edaphic conditions is thus very likely and has ultimately led to lower current levels of biomass and basal area in pre-Columbian sites. In Europe, Dambrine et al. (2007) also documented a change in understory vegetation composition along a gradient related to pH, available P, and  $\delta^{15}\text{N}$ , materializing after human impacts (Roman in the latter case).

#### *Forest composition—significant changes associated with pre-Columbian occupation*

The main gradient of the detected variation in current forest composition in our data set can be attributed to anthropization (Fig. 3), de facto an important, but underestimated, explanatory factor for deciphering

floristic patterns in terra firme forests on the Guiana Shield. This result corroborates both observations by Ross (2011), who observed an increase of useful species close to formerly highly occupied Maya settlements in Belize, and the recently published work at the scale of the Amazon basin by Levis et al. (2017). Our finding is of utmost importance for the Guiana Shield, as it is the region where Levis et al. found the lowest correlation, both in terms of abundance and in terms of richness, between domesticated species and archaeological sites. This inconsistency is probably because of the incomplete nature of the archaeological maps of the Guiana Shield. In French Guiana, for example, the archaeological map used by Levis et al. shows an overconcentration of sites in northwestern coastal savannahs. But dozens of ditched sites (including those studied here) have recently been discovered in inner French Guiana, and their number is rapidly increasing with the use of airborne LiDAR. If Levis et al. had had the opportunity to include these new sites in their analyses, their conclusions would likely have been very different. Human influence was, however, not homogeneous, as exemplified by the *Aca* western plot, which is close to the western NA control *Baf* on the DCA (Fig. 3), illustrating the influence of the main East–West biogeographical gradient of species composition in the Guiana Shield. Another possible hypothesis might be a different kind of pre-Columbian occupation for the *Aca* plot (Appendix S2). Archeological elements in this plot suggest an agricultural field, a kind of land use that might have been shorter in time than the other, more perennial, occupations (ditched/ring-ditched sites). Owing to the probably massive effort required to build ditched structures, occupation might have been longer and its influence on forest composition more pervasive. Differences might also be attributed to other cultural traits, given the wide range of cultural manifestations in human societies. Looking in more detail at plant families (Appendix S4: Fig. S1) and indicator species (Appendix S5: Table S1), five families show a clear pattern of association and 15 species appear to be closely associated with As or NAs. Some species found in the literature are closely related to the Guianese species from our plots. Notably, the genera *Oenocarpus* and *Astrocaryum* (Balée and Erickson, 2006; Junqueira et al. 2011) are known to be associated with ancient disturbed forests. Because of a relative singularity of the Guiana Shield flora, the 15 indicator species significantly differ from those observed by Junqueira et al. (2011) in the Madeira River drainage, and they might be considered as important indicators for future studies in historical ecology in the region. Moreover, this question of indicator species should be further developed to cover different anthropogenic landscapes, as each type of archaeological site may hold a different composition of indicator species. After Balée (1994), highlighting which species were associated with old fallow in the Ka’apor area, and Clement and colleagues (Clement et al. 2003, Junqueira et al. 2011) for ADE

areas, it might be interesting to collate all the works at the Amazonian scale to explore their consistency at a larger scale.

*Forest diversity—pre-Columbian occupation enhances current beta diversity*

Regarding alpha diversity, our results question the generality of Balée's hypothesis that past human occupation would have elevated species diversity of Amazonian forests (Balée 1994). More specifically, neutral alpha diversities are more difficult to interpret than neutral composition because diversity distributions between As and NAs widely overlap (Appendix S6: Fig. S1). On the contrary, the global trend, even if nonsignificant, for functional alpha diversity seems effectively to be an increase in As compared to NAs. This corroborates our results on functional composition where we found that pre-Columbian occupancy sites are today enriched in acquisitive tree ecological strategies (species with lower wood density, lower seed mass, higher specific leaf area, and lower maximal stature; Fig. 4). The current coexistence of acquisitive and conservative functional strategies automatically increases the functional alpha diversity in anthropized plots, a pattern to be linked to the intermediate disturbance hypothesis (IDH), which states that, locally, maximum alpha diversity should be obtained at intermediate disturbance levels, where diverse ecological strategies may coexist (Molino and Sabatier 2001).

Regarding beta diversity (Fig. 5), the pattern is much clearer than for alpha diversity, with neutral beta diversity significantly increasing with the proportion of anthropized (A) plots in the simulated assemblages. Although the number of species may exhibit the same pattern in A and NA plots, forests shaped by pre-Columbian societies hold different plant communities (see forest composition chapter above) adapted to different histories of human occupations (Lins et al. 2015). Consequently, beta diversity can increase in landscapes modified by past indigenous societies. Moreover, we may view past indigenous societies as intermediate disturbance agents at the landscape level and, if we admit the validity of the IDH at a regional scale (Guitet et al. 2018), the balanced coexistence of undisturbed and disturbed sites in the landscape should theoretically lead to a maximum beta-diversity level. This hump-shaped beta-diversity theoretical pattern was almost exactly obtained for functional beta diversity and may also explain, for neutral beta diversity, the saturated increase for proportions of As in the simulated assemblages above 50%. Concretely, this means that both highly disturbed and undisturbed landscapes may exhibit lower beta diversity than landscapes with complex and patchy early human occupations. In any case, the presence of pre-Columbian human occupations should be taken into consideration as an additional factor altering current diversity patterns.

*Ethnobotanical aspects, another light on pre-Columbian impacts*

Scrutinizing forest composition, the weak predominance of some peculiar families in the disturbed plots (Appendix S4: Fig. S1) as well as the presence of indicator species (Appendix S5: Table S1) can, interestingly, be well explained by ethnobotany. For example, the families most associated with As (Arecaceae, Urticaceae, and Euphorbiaceae) are known, among other things, for their edible fruits (Smith et al. 2007). Nevertheless, discussing at the family level is difficult owing to variation in uses among confamilial species that prohibits a precise analysis. Concerning indicator species, both potential uses and ecological strategies explain a large part of their relevance. Among the most numerous species, *Oenocarpus bacaba* and *Astrocaryum sciophilum* are still today esteemed for their edible fruits and probably previously constituted a large part of the diet of pre-Columbian humans (Smith 2015). Seeds of *Conceveiba guianensis* are also edible, but not used much today. Although its use might explain its abundance in As, its acquisitive ecological strategy is probably more important in shaping its current distribution.

Categories of traditional uses are heterogeneously related to the impact on the resource, and are thus complemented by the category of the plant part used. The more frequent presence of edible species on As (Fig. 6) is accompanied by the increased proportion of species whose seeds and fruits are useful (Fig. 7), and is the most salient result of this study. The 121 edible species censused in our plots, despite the lack of precise data concerning them, probably belong mainly to the semidomesticated or incipiently domesticated categories of Levis et al. (2017), and are often close relatives of some of the 85 edible species censused by these authors, extending their conclusions to the Guiana Shield. Another interesting aspect is the abundance in NAs of species used in construction (Fig. 6). The trend is clear enough to suggest new hypotheses about pre-Columbian impacts on the forest. This observation is nevertheless not confirmed by the "plant parts" category analyses (Fig. 7), which found no selective patterns for plants used for their wood. But species that have useful bark are also closely associated to NAs, giving credit to the idea that using bark on a regular basis is negatively impacting individual demographic performance (but see Amahowe et al. 2018). Conclusions are more difficult to draw for species belonging to the "medicine and magic" and "arts and crafts" categories, which showed no clear pattern. This might be explained by the fact that (1) medicinal uses are of very low impact on plants in general, because of the small quantities gathered, and that (2) crafts species are used in many different ways, some with detrimental effects, some with no or positive impacts. In the same way, the positive and significant correlation between plants used for their leaves and flowers and their abundance in As is probably explained

by the extremely frequent use of palm leaves in crafts, and it probably mainly reflects the abundance of palms in As because of the concentration of fruits and seeds related to their edibility. Use of underground organs of trees concerns only four species (*Socratea exorrhiza*, *Cecropia obtusa*, *Tovomita brasiliensis*, and *Ptychopetalum olacoides*), and the observed correlation with As certainly owes more to the acquisitive ecological status and the hyperdominance of both *C. obtusa* and *S. exorrhiza* (Ter Steege et al. 2013) than to these uses.

Nevertheless, it is difficult to disentangle human effects (direct or indirect) from geographical and environmental effects without in-depth ecological, soil, and archaeological investigations. The superabundance of acquisitive ecological strategies (mediated by long-lasting soil changes; see the foregoing) might be difficult to tease apart from compositional changes owing to differential ethnobotanical uses.

#### CONCLUSION

This work confirms for the Guiana Shield some trends observed elsewhere in Amazonia regarding the persistent effects of pre-Columbian occupation on modern forests. Our results highlight the change in current forest structure, composition, and diversity between sites formerly occupied and nonoccupied by pre-Columbian populations. By filling a major gap in our knowledge of the Amazonian forests *sensu lato* (i.e., including the Guiana Shield and other peripheral areas), it helps consider all these socio-ecosystems as directly linked together. Pre-Columbian presence (1) decreases the current levels of aboveground biomass, basal area, and tree density; (2) is responsible for significant shifts in current species composition with enrichment in species with acquisitive ecological strategies; and (3) strongly enhances the forest beta diversity at landscape scale. Moreover, different uses of tree biodiversity had contrasted impacts on the current vegetation: the edibility of some plants is likely to enhance their association with pre-Columbian sites, similar to the conclusions of Levis et al. (2017). What was expected but never demonstrated before is that pre-Columbian uses of wood for construction and of bark might also have been detrimental to some species. This approach represents an important step forward in historical ecological studies of Amazonian forests. This demonstrates that, beyond the classic ecological concept of neutral or functional diversity, taking into consideration the utilitarian diversity helps us understand past human influence on these forests. Moreover, a more holistic ethnoecological approach, co-constructed with present-day Amerindian knowledge holders, including their indigenous knowledge related to soil types and fertility, horizontal and vertical forest structure, and general forest functioning in such analyses would be a great step further. Considering the lack of data concerning terra firme archaeology in Amazonia (Stahl 2015, McMichael et al. 2017), our results show that

pre-Columbian influences on Guianan upland forests have not been as discreet and evanescent as previously thought, suggesting that similar studies in other supposedly untouched Amazonian forests, particularly in interfluvial areas, would be of great interest.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2806/supinfo>

## DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4h75q1p>.