Forest Ecology and Management 446 (2019) 317–330

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Historical landscape domestication in ancestral forests with nutrient-poor soils in northwestern Amazonia

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ABSTRACT

Past human modification of forests has been documented in central, southwestern, and eastern Amazonia, especially near large rivers. Northwestern Amazonia, and interfluvial forests there in particular, are assumed to exhibit little past human impact. We analyzed soils and floristic structure and composition of interfluvial forests located in the Içana River basin, northwestern Amazonia, to assess their degree of past human modification. Ancient Baniwa village sites, abandoned centuries ago, have given rise to “ancestral forests” with as much as 57% of all trees/palms belonging to a group of species managed currently by the Baniwa, compared to only 10% of such species in old-growth forests that are not remembered as having been inhabited or managed in Baniwa oral tradition. Participatory mapping and direct observations revealed ancestral forests to be widely distributed throughout the region, whereas old-growth forests are rare. Managed species in ancestral forests contributed 5-fold more to total tree/palm biomass than in old-growth forests. Human management has produced lasting changes in floristic composition, maintained total tree/palm biomass, and improved soil quality. This is the first study to demonstrate past human modification in Amazonian interfluvial forests, while explicitly isolating historical human management from edaphic effects on floristic structure and composition. Despite environmental limitations on human population size, posed by nutrient-poor black water rivers and acidic, sandy soils, indigenous peoples of northwestern Amazonia left a clear, lasting cultural legacy in ancestral forests. Given legal changes that threaten indigenous peoples' land rights currently under debate in Brazil, we call for a reconsideration of biodiversity conservation policies and indigenous rights in areas that show enduring legacies of management by indigenous populations.

1. Introduction

Amazonia has been occupied for thousands of years by indigenous peoples who practiced diverse environmental management strategies. Earthworks (Heckenberger et al., 2003; Watling et al., 2017), soil modification (Neves et al., 2003; Schmidt et al., 2014) and plant domestication (Clement, 1989; Levis et al., 2017) are some examples of the long-term interactions between social and natural systems that have contributed to biodiversity in Amazonia from pre-Columbian through to modern times. These processes increased the productivity of Amazonian landscapes for human needs and thus represent landscape domestication (Clement, 1999). However, the extent of such landscape-level alterations in Amazonian forests is hotly debated, and there is no consensus on where and how past indigenous populations modified Amazonian forests (Tollefson, 2013; McMichael et al., 2017). Moreover, the debate has suffered from a lack of problem-oriented in-depth studies that show clear, quantified patterning based on controlled methods.

Pre-Columbian and historical human impacts have been documented in central, southwestern and eastern Amazonia, especially along the margins of large, sediment-rich rivers (e.g., the Amazon, Madeira and Japurá/Caquetá) (Arroyo-Kalin, 2010; Clement et al., 2015; Levis et al., 2017), but less is known about such processes in the nutrient-poor forests of northwestern Amazonia, and for interfluvial regions more generally. In contrast to riverine areas, located along the margins of major rivers, interfluvial regions have been defined as upland forest areas (i.e., terra-firme forests) located between the valleys of adjacent major river basins (i.e., the Amazon, Madeira, Purus, Juruá, Negro, Japurá/Caquetá, Branco, Tapajós, Xingu, Tocantins) and which may include smaller basins (McMichael et al., 2012; Piperno et al., 2015; Stahl, 2015). Some examples of interfluvial regions in Amazonia are the Madeira-Purus interfluve (about 150–200 km wide), the Solimões-Negro (about 150–650 km wide), and the Caquetá-Negro (our

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https://doi.org/10.1016/j.foreco.2019.04.020
Received 22 February 2019; Received in revised form 12 April 2019; Accepted 14 April 2019

study region; about 150–500 km wide), all of which contain numerous tributaries and sub-tributaries.

Although some authors hypothesize that most past human populations in Amazonia were concentrated along the margins of large rivers with more abundant natural resources (McMichael et al., 2012; Bush et al., 2015; Piperno et al., 2015), others have shown that interfluvial regions harbored human populations that altered landscapes in diverse ways (Lombardo et al., 2013; Watling et al., 2017; Souza et al., 2018). The long-standing dichotomy between riverine vs. interfluvial human occupations and landscape modification has been questioned (Paz-Rivera and Putz, 2009; Stahl, 2015), and a new model of Amazonian management patterns has emerged that takes into account observed landscape legacies in some interfluvial areas (Levis et al., 2018). We know from archaeological and ethnographic research that contemporary, as well as ancient indigenous peoples have manipulated forest succession through the dispersal, concentration and protection of useful plants (Miller and Nair, 2006; Smith, 2014), both in swidden fallows close to settlements (Denevan, 2001), as well as in more diffuse agroforestry systems at greater distances (Maezumi et al., 2018). In interfluvial areas, landscape domestication probably occurred through such diffuse management processes rather than through strictly agricultural intervention (Stahl, 2015).

Ancient indigenous populations had hybrid lifestyles that included fishing, hunting, fruit gathering and forest management without necessarily developing a complete dependence on farming (Rindos, 1984; Rowley-Conwy and Layton, 2011); these populations managed forests by clearing spaces to create agroforestry systems, enriching them with useful species and suppressing undesirable species (Erickson and Balée, 2006; Shepard and Ramirez, 2011; Stahl, 2015). As recent studies have shown, patterns of composition and abundance of trees and palms in Amazonia show clear signs of human alteration going back perhaps thousands of years (Levis et al., 2017; Maezumi et al., 2018); such Amazonian forests represent domesticated landscapes. Nonetheless, many recent studies in tropical ecology have overlooked the possibility of human influence in the formation of apparently "intact" or "primary" forests (Gibson et al., 2011; Barlow et al., 2016; Betts et al., 2017), a research bias that has important implications for conservation science and policy.

The Negro River basin in northwestern Amazonia has been referred to as a "river of hunger" due to nutrient-poor black waters, sandy, acidic soils and low ecological productivity (Moran, 1991). Recent studies modeling the degree of past human landscape modification across Amazonia, based on archaeological evidence and/or rainfall seasonality (Bush et al., 2015; McMichael et al., 2015, 2017), have predicted that nutrient-poor soils in "ever-wet" interfluvial forests of northwestern Amazonia would have severely limited the possibilities for intensive agriculture, leaving the region's floristic structure and composition largely unaffected by ancient and historical human management.

Here we evaluate, for the first time, whether floristic structure and tree/palm species abundance of mature interfluvial forests of northwestern Amazonia reflect the outcome of historical human management or whether they can be explained solely by edaphic conditions. Edaphic conditions are considered to be the main factor structuring Amazonian forests on nutrient-poor sandy soils (ter Steege and Hammond, 2001). However, if humans have altered these forests in the past, we expect floristic structure and abundance of tree/palm species to be related to the presence of past human settlements, such that managed species (defined as useful species whose individuals are manipulated by humans in some way, as described by Levis et al. (2018)) will be more abundant in these "ancestral" forests than in those without evidence of human intervention.

1.1. The Baniwa people

Contemporary indigenous peoples of northwestern Amazonia form part of a complex, hierarchical, pluriethnic and multilingual social system shared between Brazil and Colombia involving over 24 ethnic groups speaking languages from four distinct cultural-linguistic families and currently numbering about 37,000 people in Brazil (Stenzel, 2017). In this region, the Içana basin is the traditional territory of the Baniwa people, who collaborated with this study and speak a group of closely related dialects in the Arawakan language family. Speakers of Arawakan languages spread throughout a vast area in pre-Colombian South America, attaining a territorial extent larger than that of the Inca empire (Aikhenvald, 2012; Eriksen and Danielsen, 2014). The wide distribution of Arawakan languages in South America and the Caribbean is attributed to a process of cultural expansion ascribed by different scholars to population movements and the spread of farming (Schmidt, 1917; Lathrap, 1970), hierarchical social systems and intensive landscape modification (Heckenberger, 2005) or inter-ethnic trade (Hornborg et al., 2005).

The Baniwa people refer to themselves as Newiki ("people") in their own language. Some Baniwa communities along the lower Içana lost their native language during the European colonization and adopted Nheengatu, a trade language derived from coastal Tupi-Guarani languages that was once spoken widely in Amazonia. The Baniwa-speaking communities of the lower and middle Içana are divided among several exogamous clans or phratries, including the Hohodene, Walipere-Dakeenai and Dzawinai (Wright, 1998). Each phratry descends from a group of mythical ancestor-brothers and claims an ancestral territory with clearly defined ecological and geographical boundaries. When people from one phratry wish to extract resources from the territories of another, they must request permission (Shepard et al., 2004). Many Baniwa myths and legends describe clan wars and negotiations due to conflicts over resources and territory (Wright, 1999, 2005). Their current system of resource management consists of shifting cultivation, fishing, forestry management, gathering of forest products and hunting.

Currently some 6500 Baniwa live in the Içana River basin (Ministério da Saúde, 2016), although in pre-colonial times this number was probably much larger. No one knows how many people lived in Amazonia prior to the arrival of Europeans; estimates range from 1 to 15 million inhabitants in 1492 (Denevan, 2014), although recent estimates of 8–10 million seem appropriate (Woods et al., 2013; Denevan, 2014; Clement et al., 2015). In northwestern Amazonia, as in other parts of the Amazon basin, invasion by Europeans initially caused catastrophic depopulation from epidemics, slavery and warfare (Andrello and Wright, 2002a; Clement et al., 2015). The Baniwa people who survived this initial decimation appear to have remained in remote interfluvial areas along tributary streams of the Içana River (Andrello and Wright, 2002b; Wright, 2005), residing in multi-family longhouses ("malocas") that housed 40–60 people (Nimuendajú, 1950; Wright, 1999; Koch-Grünberg, 2005). Due to the growing influence over the past two centuries of Christian missionaries and the Brazilian state, the Baniwa progressively abandoned their longhouses in the interior of the forests and settled in villages on the banks of the two main tributary rivers of the region, the Içana and the Ayari (Andrello and Wright, 2002b; Wright, 2005). When German ethnologist Theodor Koch-Grünberg visited the Içana basin in 1903–1905, he reported traces of ancient longhouses along tributary streams, far from the Içana River (Koch-Grünberg, 2005). Already at that time, over a century ago, these abandoned Baniwa settlements had grown into stately, mature forests whose true human legacy was only detectable with the help of the Baniwa themselves.

The Baniwa recognize three main categories of forest landscape (Abraão et al., 2010): *alápe* – seasonally flooded forests along black water floodplains (known regionally as "igapó"); *hamáliani* – stunted, open-canopy forests on sandy soils (known regionally as "campina" or "caatinga"); and *éedzawa* – closed-canopy upland forests on less sandy soils (known regionally as "terra firme", but referred to elsewhere in Amazonia as "campinarana" (Veloso et al., 1991)). The Baniwa's current shifting cultivation and agroforestry activities are focused mostly in *éedzawa* areas, due to their slightly more fertile soils (Abraão et al., 2010). We set out to test the hypothesis that past human management enriched these *éedzawa* areas with species valued by the Baniwa, transforming them, through landscape domestication, into cultural forests (Balée, 2013). The abundance of these species in northwestern Amazonia (Levis et al., 2017), the content of Baniwa oral histories (Wright, 1999, 2005; Andrello and Wright, 2002a) and historical documents (Nimuendajú, 1950; Andrello and Wright, 2002b; Koch-Grünberg, 2005), and the occurrence of soil charcoal near the Içana River basin (Saldarriaga and West, 1986; Clark and Uhl, 1987) all suggest that floristic structure and species abundance in apparently "virgin" forests (Willis et al., 2004) of the region may have been altered by past human populations.

2. Materials and methods

2.1. Study site descriptions

Field work was conducted in northwestern Amazonia, in forests of the middle basin of the Içana River, an acidic, nutrient-poor black water tributary of the Rio Negro, located in the interfluvial region between the Negro and Japurá/Caquetá Rivers; the Rio Negro, a major tributary of the Amazon, is the largest black water river in the world. The region is located on the Guiana Shield, a Precambrian formation of granitic and granulite rocks (Hammond, 2005). Due to their geological history, soils in the region are very poor and predominantly sandy, low in nutrients, oligotrophic and acidic (podzols) (Herrera et al., 1979), with vegetation ranging from closed-canopy forests (campinaranas) on less sandy soils, to open-canopy forests (campinas) on very sandy soils (Anderson, 1981). The source of the Içana River is located in Colombia, but most of the river's 580 km length is in Brazil. The average annual temperature is 25 °C and annual precipitation averages 3500 mm. The driest quarter (September-November) has an average of 765 mm of rainfall (1981–2010 data; station W68N01) (INMET, 2009). This lack of rainfall seasonality characterizes the forests of the region as "ever-wet" (Bush et al., 2015). The Içana River basin is inhabited by the Curipaco (upper Içana) and Baniwa (middle and lower Içana) ethnic groups, both speakers of closely related Arawakan languages and dialects (Andrello and Wright, 2002c).

The region surveyed is located approximately 170 km from the confluence of the Içana and Negro Rivers and 250 km in a straight line from the small city of São Gabriel da Cachoeira, capital of the municipality of the same name covering an area of 109,000 km^2 within Amazonas state. Reaching the Içana River basin is only possible by canoes or small speedboats, and navigation is difficult due to the numerous and treacherous rapids, waterfalls and whirlpools.

2.2. Experimental design

Fieldwork was conducted during three expeditions: February, 2015; April–May, 2015; and September–November, 2015, with a follow-up visit in August-September, 2018. An initial meeting with Baniwa representatives was held to explain the project's objectives and request permission to carry out research in their territory. With advice from Baniwa representatives and researchers, one Portuguese-speaking Baniwa man with prior research experience and extensive knowledge about forest management (co-author Armindo F. M. B. Baniwa) agreed to assist with fieldwork logistics, village contacts and translation. Also based on their recommendations, five study communities were chosen: *Bobope* (or Bela Vista)*, Hidzapada* (Mauá Cachoeira)*, Komalhipani* (Tucumã Rupitá)*, Owhika* (Santa Rosa), and *Ttdzealinomana* (Santa Marta). The first step in fieldwork was participatory mapping of the territory around each community by Baniwa informants who had extensive knowledge of forest landscapes and their history of management and occupation. The maps generated in this activity identified current and ancient villages and swiddens as well as sacred sites and small and medium-sized streams.

Using these maps, guided by oral histories gleaned from the literature and our interviews, and taking into account logistical considerations and the availability of willing Baniwa assistants, we selected 12 ancestral forest areas and 4 presumed old-growth forest areas to establish a total of 16 study plots. *Ancestral forests* are defined here as mature forests in the vicinity of ancient abandoned Baniwa longhouses (areas of ancient swidden fallows, gardens or house-yards in *éedzawa* areas) where modern villagers occasionally return to harvest resources. *Old-growth forests* are mature forests, also in *éedzawa* areas, with similar canopy structure, but where modern Baniwa identify no ancestral settlements. Mature forests are defined as forests in a late stage of succession that are subject only to localized disturbances, such as tree falls or seasonal flooding (Chazdon, 2014). The smaller number of old-growth forest plots in the sample owed to the difficulty of locating sufficient forest areas where the Baniwa recognized no ancient settlements, an observation that in itself attests to the extent of historical Baniwa interventions in the regional forest landscape.

For each plot, edaphic conditions were measured: sand content, soil pH, phosphorus and charcoal concentrations, and effective cation exchange capacity (ECEC) (see Section 2.3 for details). Forest community structure was evaluated in terms of the relative density, abundance, and basal area of managed tree/palm species; overall tree/palm density, abundance, and basal area; and ecological importance value (EIV). The observed relative abundance of managed species was then projected to the landscape scale using a computerized model to provide a view of the potential extent of domestication in interfluvial forests across the Baniwa territory.

2.3. Field sampling

In addition to our Baniwa research collaborator and co-author Armindo F. M. B. Baniwa, two Baniwa assistants from each study community were chosen for their extensive knowledge of tree/palm names to assist us in collecting data in the territories of their respective communities. In areas identified through participatory mapping and oral histories, ancestral or old-growth forest plots of 10 × 72 m (720 m^2 or 0.072 ha) were established for floristic inventories, measuring the circumference of all trees/palms $\geq$3.18 cm DBH (diameter at breast height, ~130 cm), i.e., 10 cm CBH (circumference at breast height). For our specific purpose of analyzing local disturbances, this plot size is considered appropriate in Amazonia (Oliveira et al., 2014). In order to assess the local legacy of disturbance related to human management, we needed a set of small plots representing local disturbance dynamics at a scale appropriate to historical Baniwa habitation and management activities (see Chazdon, 2014). In areas near our study region, floristic inventories have used plots of 300 m^2 to analyze historical human disturbance dynamics with a satisfactory representation of forest structure and composition (Saldarriaga et al., 1988). Therefore, we considered 720 m^2 plots to be adequate for the purpose of this study.

The indigenous names and uses of each tree/palm were provided by assistants. Baniwa language terms are written using the orthographic conventions presented by Ramirez (2001). Results of prior ethnobotanical and botanical studies carried out in the same region (Silva, 2004; Abraão et al., 2008, 2010; Stropp et al., 2014) were used as a guide to streamline field identifications. Botanical vouchers were collected and taken to the herbarium at the National Institute of Amazonian Research (INPA, Manaus, AM) for expert identification, and were then deposited in the Herbarium of the Federal Institute of Education, Science and Technology of Amazonas (EAFM/IFAM, Manaus, AM). Botanical vouchers collected in previous studies in the same region are deposited in three herbaria: EAFM (two campuses, São Gabriel da Cachoeira and Manaus) and INPA (Manaus).

Two soil samples were collected in each plot using a post-hole digger (~15 cm in diameter), one at the beginning and one at the end of the plot. Each sample was divided into two subsamples: 0–20 cm (after discarding leaf litter and surface roots) and 20–60 cm depth. When logistically possible (i.e., when we still had time before nightfall in the forest), the 80–100 cm layer was also collected. Two additional ancestral forests that were not botanically inventoried were sampled for charcoal in the 20–60 and 80–100 cm layers. In each of these extra ancestral forests, two holes separated by 70 m were dug and soil was collected. The current study did not have sufficient financial resources for radiocarbon dating. Thus, the separation of soil samples into two layers (0–20 and 20–60 cm) was inspired by a previous study of soil charcoal rediocarbon dates in a nearby region that conclude that charcoal found 20 cm and deeper tended to be of pre-Columbian origin, while charcoal in the upper soil layer (0–20 cm) tended to be of more recent, post-colonial origin (Saldarriaga and West, 1986). However, as mechanical mixing of soil from different layers can occur depending on the depositional context, using charcoal depth as a proxy for actual radiocarbon dates is problematic. Charcoal samples have been stored for potential dating in future studies.

Geographical coordinates of all sample areas were recorded at the midpoint of each plot with a Garmin eTrex H GPS. Distances of plots to the Içana River, to the corresponding villages that "own" each ancestral territory, and to the nearest watercourse (navigable by canoes) were calculated using the "ruler" tool in Google Earth 7.1.5. Distances travelled during fieldwork to reach the plots from villages were calculated with the "route" tool of the GPS unit.

2.4. Laboratory analysis of soil and charcoal

Soil samples were taken to the Thematic Laboratory of Plants and Soil at INPA. The samples were air dried, broken up, sieved through a 2 mm mesh, and homogenized. The volume of each sample was measured using a 10^3 cm^3 glass cube, where the width (10 cm) and length (10 cm) were multiplied by the height of the soil sample (in cm) in the cube. In each sample, pieces of charcoal larger than 1 mm were removed with tweezers and weighed. Chemical (pH [H2O], P, K, Ca, Mg, Al) and physical (total amount of sand) analyses were performed in the 0–20 cm layer using the methods of EMBRAPA (Donagema et al., 2011). Two charcoal samples were discarded after they fell to the ground during the analysis.

2.5. Statistical analysis

To compare floristic composition between plot, we used non-metric multidimensional scaling (NMDS) (McCune and Grace, 2002) based on the relative abundance of the 46 most abundant species in all plots (72% of the total abundance), applying the Bray-Curtis dissimilarity index (Faith et al., 1987). Using only the most abundant species avoids the "noise" generated by rare species in this sort of gradient analysis (Gauch, 1982; Marchant, 2002), although rare species are important for ecological quality studies (Lenat and Resh, 2001). Rare species are defined as those that constitute $< 0.5\%$ of relative abundance in relation to the total of individuals in all plots. In the NMDS, ordination in one dimension explained 67% of the variation with a stress of 0.27, a value not considered adequate for analysis of community ecology (McCune and Grace, 2002). The ordination in two dimensions explained 83% of the variation in species relative abundance with a stress of 0.14, a value considered satisfactory (McCune and Grace, 2002). Adding additional dimensions contributed little to increase the percentage of variation explained. The NMDS axes, which describe dissimilarity between plot in relation to species relative abundance, were used as dependent variables in a multivariate analysis of covariance (MANCOVA) to test the relationship between species relative abundance and edaphic variables as well as presence/absence of human management. An exploratory analysis was carried out to select the edaphic variables with independent effects on the NMDS axes. The final MANCOVA model included soil sand proportion and soil pH as quantitative independent variables, and presence/absence of historical Baniwa management (ancestral vs. old-growth forests) as a categorical independent variable. The NMDS was performed using R 3.5.0 software (Crawley, 2012). The MANCOVA analysis was performed using SPSS 17.0 software (Field, 2009).

Edaphic variables analyzed included soil pH, phosphorus (P) content (mg/kg), effective cation exchange capacity (ECEC) (Ca + Mg + K + Al cmol/kg), charcoal (mg/cm^3) and sand content (%), all determined for the 0–20 cm layer; soil charcoal concentration was determined for all soil layers. Differences between ancestral and old-growth forests in terms of soil quality (pH, phosphorus, ECEC and sand content), charcoal concentration, and community structure (total density, abundance, and basal area, and relative abundance of managed species) were tested with Student's *t* test when data were normally distributed, and with the Mann-Whitney test when distributions were non-normal. Simple non-linear regressions (quadratic functions) were used to evaluate the relationships between the distance to the Içana River (independent variable) and charcoal concentration at both 0–20 cm and 20–60 cm depth (dependent variables). Simple linear regressions were used to evaluate the relationships between charcoal concentration (0–20 depth) (independent variable) and soil pH (dependent variable). The analyses were performed using SPSS 17.0 software (Field, 2009).

To calculate the mean age of forests in our plots, we used a model created by Saldarriaga et al. (1988) for the Rio Negro basin in a study area less than 150 km from our own, with similar floristic structure and composition. The model, specific to this region, is a logarithmic regression: $\ln(Y) = 1.75 + 0.34 * \ln(X)$, where Y is the mean basal area (expressed as $m^2 ha^{-1}$) and X is the minimum successional age of the forest plot (years). Although basal area (Y) is expressed as m^2 per hectare to facilitate comparisons, the authors used small plots (300 m^2 or 0.03 ha), and thus forest age (X) is attributed only to those small plots areas, not to larger, hypothetical 1 ha areas. According to this model, closed-canopy mature forests at their study site have a mean basal area of 34.8 $m^2 ha^{-1}$ and a minimum age of 190 years. Using this model, we calculated the mean minimum successional age for the 0.072 ha plots in our study area.

The relative density, abundance and basal area of managed species were calculated as a percentage of the total density, abundance and basal area of each plot, respectively. The Ecological Importance Value (EIV) of each species was calculated for ancestral and old-growth forests. The EIV is composed of the sum of frequency, dominance and density of species (Mueller-Dombois and Ellemberg, 1974); the value indicates the importance of a particular species in the tree/palm assembly. Here EIV was used to rank the importance of species within forest types. To understand if the signature of past human management in the forests is related to the distance to the major river of the local basin, we used simple linear regressions relating the distance of plots to the Içana River (independent variable) to each of the following dependent variables: relative density, abundance, or total basal area of managed species, and relative abundance of useful, important, or edible species. To understand if the signature of past human management of the forest is related to the closest watercourse in the vicinity, we used simple linear regressions relating the distance of plots to the nearest watercourse navigable by canoe (independent variable) to relative density, abundance, or total basal area of managed species (dependent variables). The analyses were performed using SPSS 17.0 software (Field, 2009).

The relative abundance of managed species was projected for forests in Baniwa territory throughout the Içana River basin (see Andrello and Wright, 2002a for a contextualization of the Baniwa ancestral territory) using the average values of the abundances of managed species for both ancestral and old-growth forests (more details in Section 3.3). Although our indigenous informants affirm that old-growth forests are rare in the Içana River basin, for purposes of modeling the degree of landscape domestication, we assume that both forest types (ancestral and old-growth) have equal occurrence in the terra firme (*éedzawa*) forests of the Içana River basin. Thus, our estimates for the degree of landscape domestication are very conservative. The maps derived from this projection were produced in ArcGIS 10.4 software (Johnston et al., 2001).

2.6. Interviews

Semi-structured interviews about management practices, historical occupation of the region, mythology and plant uses were conducted with one or more men, aged 30–84 years, in each community, totaling seven interviews of this type for the study. Semi-structured interviews based on directed but open-ended questions offer greater flexibility to probe oral histories and other more general aspects of local environmental knowledge (Bernard, 1988). Structured interviews, involving the listing and description of useful trees/palms and specific practices for managed tree/palm species, were conducted with 35 adults (25 men, aged 22–78 years, and 10 women, aged 17–49 years) from the five communities.

2.7. Research ethics

Because the research was done in an indigenous territory and involves traditional knowledge, we obtained authorization from Brazilian Federal authorities: National Indian Foundation (Fundação Nacional do Índio - FUNAI) – N°. 0270/GAB/CR-RIO NEGRO/2015, and National Council for Ethics in Research with Human Subjects (Conselho Nacional de Ética em Pesquisa com Seres Humanos - CONEP) – CAAE N°. 45373015.2.0000.0006. The Federation of Indigenous Organizations of the Negro River (Federação das Organizações Indígenas do Rio Negro - FOIRN) and the Indigenous Organization of the Içana River Basin (Organização Indígena da Bacia do rio Içana - OIBI) authorized research in their territory via FOIRN protocol n° 20. At each village, the study was explained to village leaders and members, who all consented to the research through their representatives. We obtained prior informed consent for all informal, semi-structured and structured interviews from each informant immediately before the interview, emphasizing the fact that they were under no obligation to participate. According to the guidelines of Brazil's environmental agency ICMBio, plant and soil collections outside of natural protected areas require only authorization from the land owners or other holders of use rights over the land, in this case, the indigenous authorities – FOIRN and OIBI.

3. Results

3.1. Formation of ancestral forests, management practices and managed species

Some of the Baniwa people we interveiwed referred to ancestral forests as places that the "*grandparents of their grandparents*" inhabited. Such information has been passed down through generations, and some older people remembered having seen ceramic fragments, stone axes and ancient house posts in the vicinity of these locations – in particular, posts made of *Minquartia guianensis* (Olacaceae) tree trunks. Taking into account these interviews, as well as Baniwa oral histories from the ethnographic literature (Wright, 1999, 2005; Andrello and Wright, 2002a, 2002b) and historical documents (Nimuendajú, 1950; Koch-Grünberg, 2005), we estimate that the ancestral forests we studied emerged around ancient settlements along smaller streams that have been abandoned for at least 200 years, or approximately six generations ago.

The modern Baniwa, who now live along the main course of the Içana and Ayari rivers, re-use their current swidden sites cyclically, creating a dynamic patchwork of swidden fallows and forests in different stages of succession. Recent and historical swidden sites that have been abandoned and grown over with successional forests are refered to as *heñame* ("place that has been used"), while mature forests that have grown around ancient settlements are referred to as *dzakaremi* ("old dwelling"). Here, what we refer to as "ancestral forests" are forests located in the vicinity of *dzakaremi*, which encompass habitation sites as well as ancient swidden fallows (*heñame)*. Forests with no known history of Baniwa occupation are referred to as *makakanaweriko* ("immemorial forest"), which we call "old-growth forests".

Although it is impossible to observe the processes that originally contributed to the formation of ancestral forests, certain analogs of these processes are visible in and around current Baniwa settlements: the disposal of charcoal, broken ceramics, vegetable skins and pulp, fruits and seeds, animal bones, construction materials, house posts, rotten roof thatch and other artifacts around the edges of the habitation area; concentrations of discarded seeds from edible fruits adjacent to the household, some of which sprout, turning into seedling banks; the care and cultivation of such seedlings, whether intentionally planted or growing from trash heaps, including fertilizing them with charcoal from hearth fires and other organic remains; the resulting growth of a small island of vegetation, mostly edible and useful species; the enrichment of soil in the immediate vicinity of modern households due to the accumulation of charcoal and other organic material, even on infertile, dune-like white sand soils; and, in the vicinity of abandoned and current households, patches of mature fruit trees/palms, including some of the same managed species (see below) found in ancestral forest plots, as well as recently introduced species such as coconut palm (*Cocos nucifera*), cupuaçu (*Theobroma grandiflorum*; Malvaceae) and the "Pará" Açaí palm (*Euterpe oleracea*) (see Appendix A, Figs. A1–A13). Other modern Baniwa agroforestry management practices we observed or heard mentioned in the field include: transplanting seedlings to gardens or swiddens, with periodic weeding or burning to facilitate growth; protection of certain tree species during the felling and burning of swiddens; intentional or accidental seed dispersal in house-yards and along forest trails; clearing of undergrowth around useful trees in swidden fallows and mature forests, whether spontaneous or transplanted; elimination of competing plants that do not interest them; and use of small-scale fire to control species turnover during vegetative succession.

We identified a total of 92 tree/palm species currently used by the Baniwa, not all of which are managed. Many of these same species are abundant in local forests (Appendix B, Fig. B1). Based on interviews with the Baniwa, we classified these among four nested categories (Fig. B1): "useful species" (all 92 species), which are those cited with any utility (food, construction, fuel, medicine, fish bait, hallucinogen, handicraft etc.); "important species" (71 species), encompassing useful species cited by informants as indispensable to their livelihood; "edible species" (33 species), cited specifically for the use category of edibility; and finally "managed species" (14 species), which encompasses only useful species (all with edible fruits) that are managed in some way. Although many studies consider the abundance of "useful species" to assess the degree of human impact in forests, we choose to focus only on "managed species" as relevant to forest composition near ancient settlements; many otherwise "useful" species are not actively managed, so their abundance may not be related to human activities. The 14 species identified as "managed" were: *Tapirira guianensis* (plant family: Anacardiaceae; Baniwa name: **Maipanalhi**; Brazilian popular name: Tapiriri)*; Couma* sp. (Apocynaceae; **Widzoli**; Sorva;)*; Attalea maripa* (Arecaceae; **Weettiri**; Inajá)*; Euterpe precatoria* (Arecaceae; **Manakhe**; Acaí)*; Oenocarpus bacaba* (Arecaceae; **Pooperi**; Bacaba)*; Oenocarpus bataua* (Arecaceae; **Ponama**; Patauá)*; Dacryodes* sp. (Burseraceae; **Oowada**; Uapixuna)*; Pourouma cucura* (Cecropiaceae; **Idzepo**; Cucura)*; Inga* sp. 1 (Fabaceae; **Paate**; Ingá); *Inga* sp. 2 (Fabaceae; **Itsipateni**; Ingá)*; Humiria balsamifera* (Humimriaceae; **Maporotti**; Umirí)*; Poraqueiba sericea* (Icacinaceae; **Doomali**; Umarí)*; Theobroma subincanum* (Malvaceae; **Mawiloda**; Cupuí); *Pouteria ucuqui* (Sapotaceae; **Hiniri**; Ucuquí).

All managed species were cited as sometimes transplanted to gardens and swiddens. Other management practices apply to varying degrees depending on the species, for example the wild cacao relative

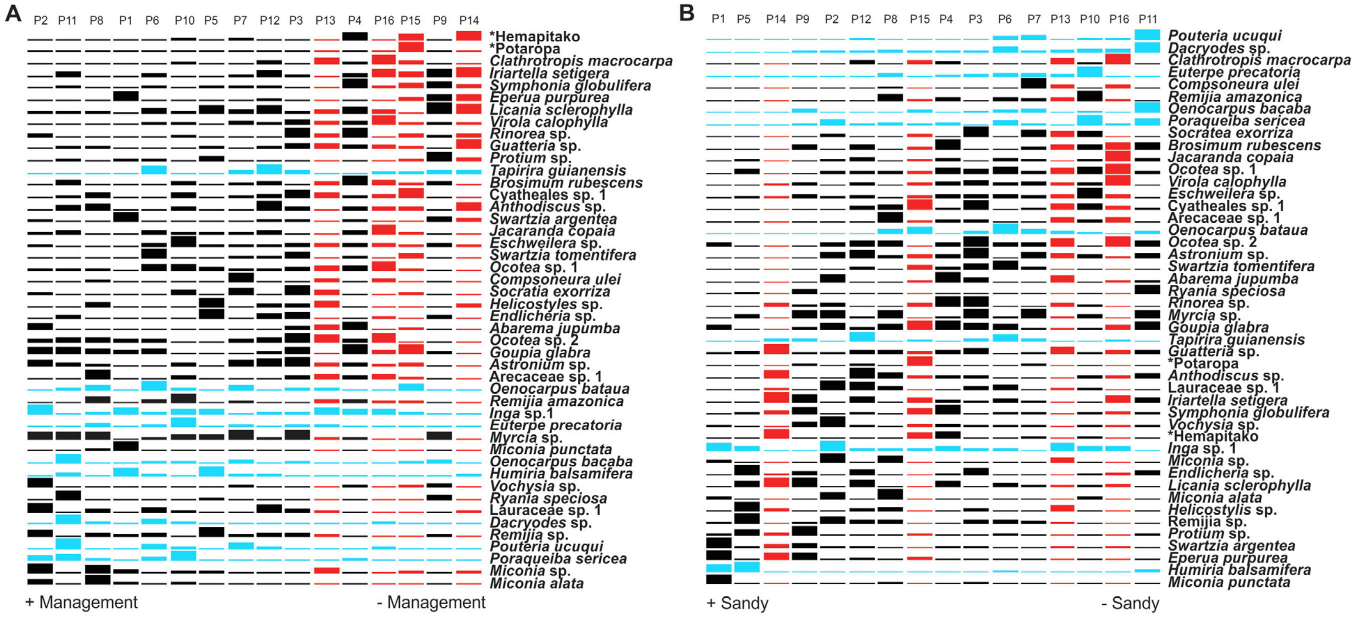

Fig. 1. Gradients of relative abundance of species ordered by NMDS. A, ordered by axis 2; B, ordered by axis 1. The 46 most abundant species in the 16 plots (trees and palms ≥ 3.18 cm DBH) were used for the analysis and represent 72% of total abundance (Table C4). The number above the columns (P1 – P16) refers to plot codes (N = 12 in ancestral forests and N = 4 in old-growth forests). Species names are listed to the right of each chart; two unidentified species are marked with an asterisk (*), with only the Baniwa name given. The size of the bars within columns represents the relative abundance of each species in that plot in relation to its total abundance in all plots. Black bars indicate non-managed species in ancestral forests (plots 1–12), red bars indicate non-managed species in old-growth forests (plots 13–16) and blue bars represent managed species. Ancestral and old-growth forests occur throughout the floristic gradient related to sand content (MANCOVA, $P = 0.004$) (B), but they are grouped differently in the gradient related to past human habitation (MANCOVA, $P = 0.007$) (A). As can be seen by the concentration of blue bars towards the bottom left of Fig. 1A, ancestral forests show a much greater abundance of managed species (Fig. B2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Theobroma subincanum grows conspicuously along forest trails, a fact the Baniwa attribute to their own habit of consuming the fruit and discarding the seeds as they walk along trails, while *Humiria balsamifera* abounds in areas subjected to fire management (see Levis et al., 2018 for a discussion of such management practices across Amazonia). We cannot know how stable species preferences and management practices have been through time; indeed, we noted the presence of several recently introduced species to the group of useful trees being managed around modern Baniwa settlements (coconut, cupuaçu, "Pará" Açai etc.). However, given the widespread use of many of the same native local species by diverse indigenous peoples of the upper Negro River region (Schultes, 1977; Milliken et al., 1999; Silva et al., 2007; Gonçalves, 2017), we assume some degree of continuity over recent centuries.

3.2. Relative abundance of species

NMDS captured 83% of floristic variation, and its axes (which represent the dissimilarity among plots in relation to the species' relative abundances) were related to presence/absence of past human habitation ($P = 0.007$) and soil sand content ($P = 0.004$) (Fig. 1). Other edaphic variables (ECEC, phosphorus and pH) were not significantly related to the gradient of species relative abundance ($P > 0.05$ in all cases).

The gradient related to presence/absence of past human habitation shows a separation of ancestral from old-growth forests (Fig. 1A). This separation is due to the fact that old-growth forests are similar to each other in terms of high/medium relative abundance of some non-managed species, located at the top of the gradient, that have low relative abundance or are absent in most ancestral forests (with the exception of plots 4 and 9). At the same time, ancestral forests are similar to each other in terms of the relative abundance of some species, located at the base of the gradient, that have low relative abundance or are absent in old-growth forests. The base of the gradient contains both non-managed and managed species, which indicates that past human management contributed to the floristic difference between ancestral and old-growth forests. Some ancestral forests contain high abundances of species from the middle of the gradient (plots 3 and 12), suggesting that they are transitional ancestral forests that bear less human legacy than others.

Relative abundance of species also varied along a gradient of soil sand content, but both ancestral and old-growth forests occur along the whole gradient (Fig. 1B). Ancestral and old-growth forests share relative abundance of some common non-managed species, such as *Swartzia argentea* (Fabaceae), *Eperua purpurea* (Fabaceae) and *Licania sclerophylla* (Chrysobalanaceae) in sandier soils; *Iriartella setigera* (Arecaceae), *Symphonia globulifera* (Clusiaceae) and *Goupia glabra* (Goupiaceae) in moderately sandy soils; and *Brosimum rubescens* (Moraceae), *Ocotea* spp. (Lauraceae) and *Remijia amazonica* (Rubiaceae) in less sandy soils. This shows that some ancestral forests are more similar to certain old-growth forests due to sharing of groups of species adapted to either less or more sandy soils, and that the Baniwa managed forests on all sort of soils, irrespective of sandiness.

Analyzed as a group, the 14 managed species comprised as much as 57% (mean 21.5% ± 15.3 s.d.) of the relative species abundance of ancestral forests, compared with a maximum of 10.5% (mean 7.7% ± 3.8) for old-growth forests ($P = 0.030$, Fig. B2; Appendix C, Table C1). Analyzed individually, managed species (only the nine species that are part of the 46 most abundant species shown in the Fig. 1) show higher relative abundance in ancestral forests than old-growth forests ($P = 0.006$, Fig. B3; Table C2), with the exception of *Oenocarpus bataua* and *Inga* sp. 1. The most abundant managed species varied among ancestral forests (Table C2), perhaps reflecting historical contingencies, soil conditions and/or micro-variations in local cultural preferences. For example, three species at the top left of Figure B3, *Dacryodes* sp., *Poraqueiba sericea* and *Oenocarpus bacaba*, respectively, were very abundant in some ancestral forests with low/medium sandiness (Fig. 1B; Table C2, plots 2, 6, 7, 8, 10 and 11). On the other hand, in ancestral forests on sandy soils *Humiria balsamifera* dominates (Fig. 1B; Table C2, plots 1 and 5). Managed species were absent from the top five most abundant species in old-growth forests, except for *Dacryodes* sp. in plot 16 (Table 2). Managed species represent 31.9% of the species with relative abundances > 5% (per plot) in ancestral forests compared with 7.1% for old-growth forests (Table C2), a 4.5-fold difference. Thus, despite expected variation in species abundance/composition due to soil condition and historical contingencies, the overwhelming presence of managed species in ancestral forests, and their relative absence in old-growth forests, suggests a strong relationship with past management by Baniwa ancestors (Fig. 1A).

Four managed species, *Poraqueiba sericea*, *Dacryodes* sp., *Oenocarpus bacaba* and *Humiria balsamifera*, accounted for 18.7% of the ecological importance value (EIV) in ancestral forests and were among the ten most important species for these forests; by contrast, only one managed species, *Dacryodes* sp., was found among the ten most important species for old-growth forests, accounting for only 2.3% of EIV (Fig. B4). The five most abundant species in ancestral forests (of which three are managed) accounted for 25.5% of the total tree/palm abundance in these forests – *Virola calophylla* (8.1%; Myristicaceae), *Dacryodes* sp. (4.5%), *Poraqueiba sericea* (4.4%), *Vochysia* sp. (4.4%; Vochysiaceae) and *Oenocarpus bacaba* (4.2%) (Fig. 2A). In old-growth forests, the non-managed species *V. calophylla* alone accounted for 17.3% of the total abundance (note its exceptionally high abundance in plot 16; Table C2) and was the most abundant species in three out of four old-growth forest plots (Fig. 2B; plots 13–16 in Table C2).

3.3. Tree and palm community structure

Ancestral and old-growth forests did not show significant differences for total species density (N = 12 and 4, and mean ± s.e.m. = 56.8 ± 4.1 and 63.5 ± 7.2 species per 0.072 ha, respectively), stem abundance (211 ± 8.3 and 227.3 ± 15.9 individuals per 0.072 ha) and tree/palm total basal area (2.98 ± 0.22 and 2.53 ± 0.11 m^2 per 0.072 ha) ($P > 0.05$ in all cases, Fig. B5); by scaling up and expressing our values as $m^2 ha^{-1}$ (see Section 2.5 for more details; original data in Table C1), tree/palm basal area measured in ancestral forests was 41.4 $m^2 ha^{-1}$ and in old-growth forests 35.1 $m^2 ha^{-1}$. Managed species accounted for 40% of basal area across ancestral forests, compared with 8% for old-growth forests (a five-fold difference; Table C1). The three dominant species in terms of basal area in ancestral forests are managed: *Poraqueiba sericea* (16%), *Dacryodes* sp. (9%) and *Oenocarpus bacaba* (6.4%) (Fig. 2C). Even though their

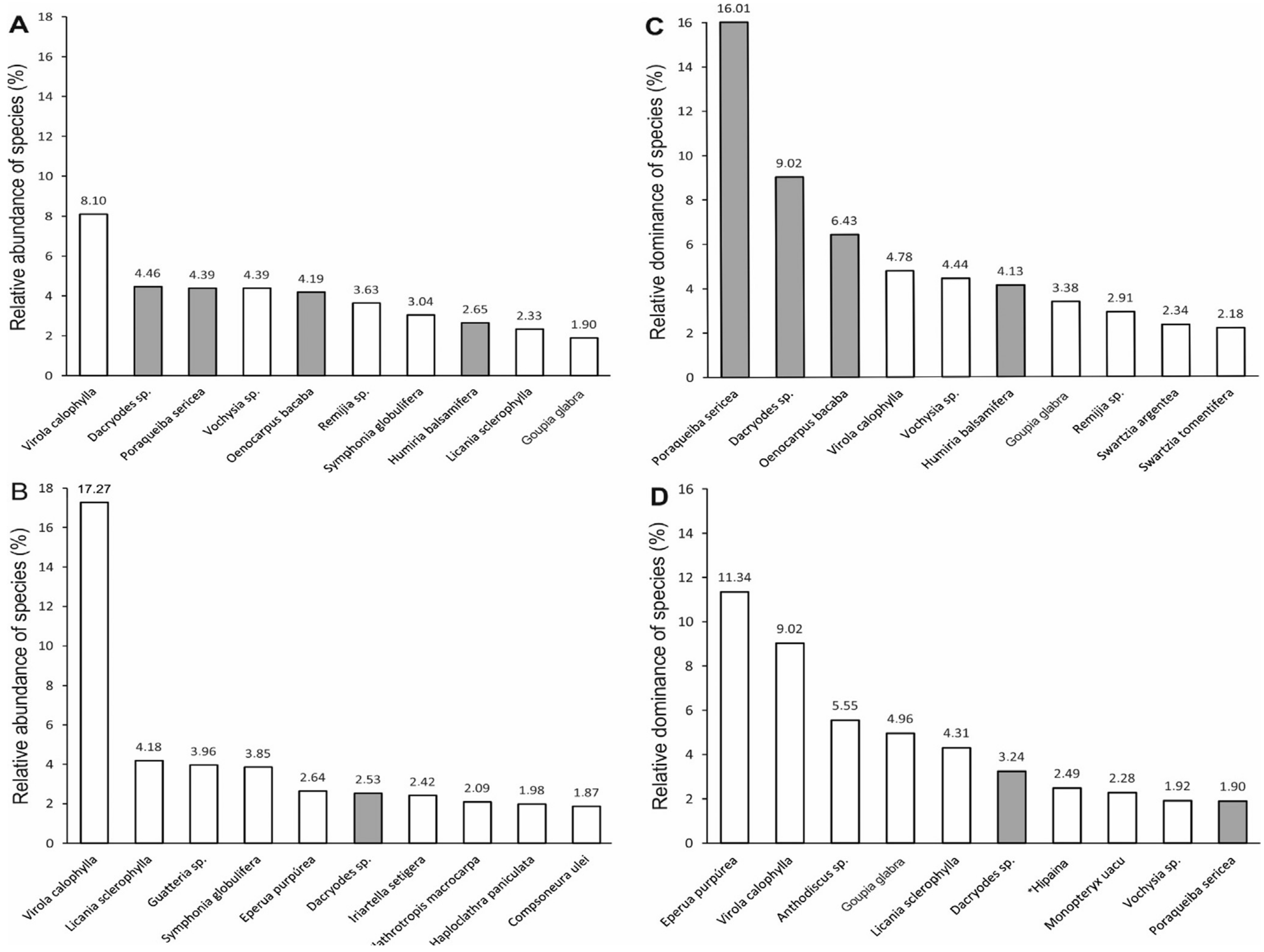

Fig. 2. Relative abundance and dominance of the ten most abundant and dominant species, respectively (bars in grey represent managed species). A, relative abundance of the ten most abundant species in ancestral forests; B, relative abundance of the ten most abundant species in old-growth forests. Relative abundance refers to the number of stems of a given species in relation to the total number of stems in ancestral forests (A) or old-growth forests (B). C, relative dominance of the ten most dominant species in ancestral forests; D, relative dominance of the ten most dominant species in old-growth forests. Relative dominance refers to the contribution in terms of biomass (basal area) of a given species in relation to the total basal area in ancestral forests (C) or old-growth forests (D). Individually, managed species clearly dominate ancestral forests in terms of biomass (C and D). Ancestral forests show more evenly distributed floristic diversity than old-growth forests, where V. calophylla prevails (A and B). One unidentified species is indicated by an asterisk (*) and its Baniwa name.

abundance is sometimes moderate to low in some ancestral forest plots, these species were present among the 5 most dominant species in these plots due to their often large diameter (e.g., plots 4, 8, 9 and 12, Table C2); the third quartile (a descriptive statistics that represents the middle value between the median and the highest value of the data set, that is a number for which 75 % of the data is less than that number) of DBH for these species were 29.9, 16.24 and 19.1 cm, respectively, compared to 10.5 and 12.9 cm for *Virola calophylla* and *Vochysia* sp., the fourth and fifth ranked species, respectively (Fig. 2C). In old-growth forests the three dominant species in terms of basal area are not managed: *Eperua purpurea* (11.3%), *Virola calophylla* (9%) and *Anthodiscus* sp. (5.6%; Caryocaraceae) (Fig. 2D). The managed species *Dacryodes* sp. appears in sixth place for old-growth forests (3.24%) mainly because of its dominance in plot 13, and *Poraqueiba sericea* (another managed species) appears in tenth place (1.9%) mainly because of the prevalence of a few large individuals in plot 15 (Table C2). Nonetheless, in general, managed species do not appear in the top five dominant species for old-growth forest individual plots (Table C2).

The relative density, abundance and basal area of managed species do not decrease up to 12.7 km from the Içana River, nor as far as 750 m from medium and small watercourses (including the Içana and its tributary streams) ($P > 0.05$; Fig. B6). The most distant ancestral forest surveyed, 12.7 km in a straight line from the Içana River, is recognized locally as the site of an ancient longhouse whose descendants currently reside in the village of *Bobope* (Bela Vista), located on a margin of the Içana River about 19 km from the ancient longhouse (Table C3). Combining this cartographic information with our botanical data, we project that managed species represent about 15% (calculation in Fig. 3) of the species abundance of all closed-canopy mature forests located as far as 19 km from any currently existing village, and as far as 750 m from any watercourse (Fig. 3), suggesting a high degree of landscape domestication. Reinforcing the results of this projection, satellite imagery of Baniwa territory beyond the sampled region also shows intensive management near many small watercourses (Fig. B7, colored boxes). Though some degree of regional and historical variation would be expected among the 110 modern Baniwa villages, and between past and present practices, for purposes of this study we are assuming historical stability and regional homogeneity in terms of preferences and practices towards the most intensely used and managed tree and palm species.

3.4. Edaphic conditions and archaeological evidence

Soil pH and charcoal concentration in the top 20 cm were related ($R^2 = 0.67$, $P < 0.001$, $N = 15$, Fig. 4), and both were higher in ancestral when compared to old growth forests ($P = 0.052$, Fig. B8A; $P = 0.009$, Fig. 4), indicating that historical Baniwa management reduced soil acidity. Ancestral and old-growth forests showed no differences in soil quality with respect to ECEC, phosphorus, and sand concentration ($P > 0.05$ in all cases, Fig. B8). These results indicate that although pH was higher in ancestral than old-growth forests, overall edaphic conditions are similar in these forests.

Charcoal concentrations were higher for ancestral than old-growth forests in the top 20 cm soil layer, which, together with our surface observations of archaeological remains in ancestral forests, strongly reinforces the role of Baniwa management activities at historically occupied settlements in shaping these soils and the forests that have since grown there. Below that depth (20–60 cm), charcoal concentrations were lower, and similar for ancestral and old-growth forests (Fig. 5). Charcoal was found as deep as 80–100 cm in some localities. Charcoal concentration in the 0–20 cm and 20–60 cm soil layers does not decrease with distance from the Içana River ($P = 0.305$ and $P = 0.559$, respectively; Fig. B9), as some authors would have predicted under the assumption of limited human occupation in interfluvial areas (Bush et al., 2015). Although there is a gap in the models presented in Figs. B9 and B6 (between approx. 5–11 km), we have confidence in their predictive power due to the existence of many ancestral forests in these regions (Fig. B7). High values for soil charcoal and relative abundance, density and basal area of managed species found even in the most remote study plots (> 11 km from the main course of the Içana River) further reinforce the predictive value of the models.

In addition to charcoal in the soil, and confirming Baniwa observations about the presence of ancient long houses at these sites, we encountered stone axes, potsherds and wooden house posts of *Minquartia guianensis* on the forest floor (and in the vicinity of the forest plots) in all 12 plots in ancestral forests (some such vestiges are presented in Fig. B10). In old-growth forests, by contrast, no such surface evidence of ancient habitation was observed. *Minquartia guianensis* is one of the most resistant and durable woods of the Amazonian flora, and for this reason house posts made with it can persist for centuries (Silva and Leão, 2006; note: informants confirmed these were house posts, not standing dead trees, by digging down to reveal the cut base). Together, these findings show that Baniwa ancestral forests are indeed associated with archaeological sites on abandoned settlements.

4. Discussion

We have shown that interfluvial forests far from major Amazonian rivers can bear lasting legacies of past human management, manifest in soil modification and the concentration of useful managed species in areas of ancient and historical human occupation. Our results contradict prior studies that question any enduring legacy of past human management on modern floristic structure and abundance of species in Amazonian interfluvial forests, and the northwest Amazon region specifically (McMichael et al., 2012; Piperno et al., 2015). Moreover, recent studies drawing on climatic data and archaeological evidence failed to identify the Içana River basin as a likely area for cultural forests, instead predicting “natural” forests in the region (Bush et al., 2015; McMichael et al., 2015, 2017). We show how multiple approaches drawn from Historical Ecology (McClenachan et al., 2015), combining ecological sampling, ethnographic methods, archaeological surveys and remote sensing are required to detect and document cultural forests. Much of the research carried out on plant biodiversity patterns has made the more or less implicit assumption that the chosen study plots are “intact” and “primary” and consequently largely free of historical human influences (Gibson et al., 2011; Barlow et al., 2016; Betts et al., 2017). The present study contributes to a growing body of work that challenges such assumptions (Erickson and Balée, 2006; Shepard and Ramirez, 2011; Clement et al., 2015; Levis et al., 2017). Given this growing body of evidence, studies of biodiversity patterns in Amazonia cannot continue to ignore the possibility that past human occupation and management may have influenced species communities, even in apparently uninhabited areas (Chazdon, 2003).

This is the first study isolating human management effects from edaphic effects in the floristic structure and abundance of species of ancestral and old-growth forests in interfluvial forest areas of Amazonia. Our work echoes the study of Paz-Rivera and Putz (2009), who suggest that past human management may have enriched interfluvial forests with useful trees in the Bolivian Amazon, although their work was unable to demonstrate a statistically significant effect, as ours does. Our results show that differences in relative abundance of species between ancestral and old-growth forests are not related to soil conditions per se, but rather to past human management. This corroborates the assumption that intra-regional differences in Amazonian forest plots are best explained by the differential impact of land-use history on forest recovery (e.g., traditional shifting cultivation, agroforestry etc.) rather than by soil fertility (Moran et al., 2000). Overall, of the five most abundant species in our plots (ancestral plus old-growth forests), three are managed (Table C4), reflecting the legacy of historical human management on floristic structure and species abundance in the region. These results reinforce the findings of recent studies into human factors behind species hyperdominance in Amazonia: four of the ten most

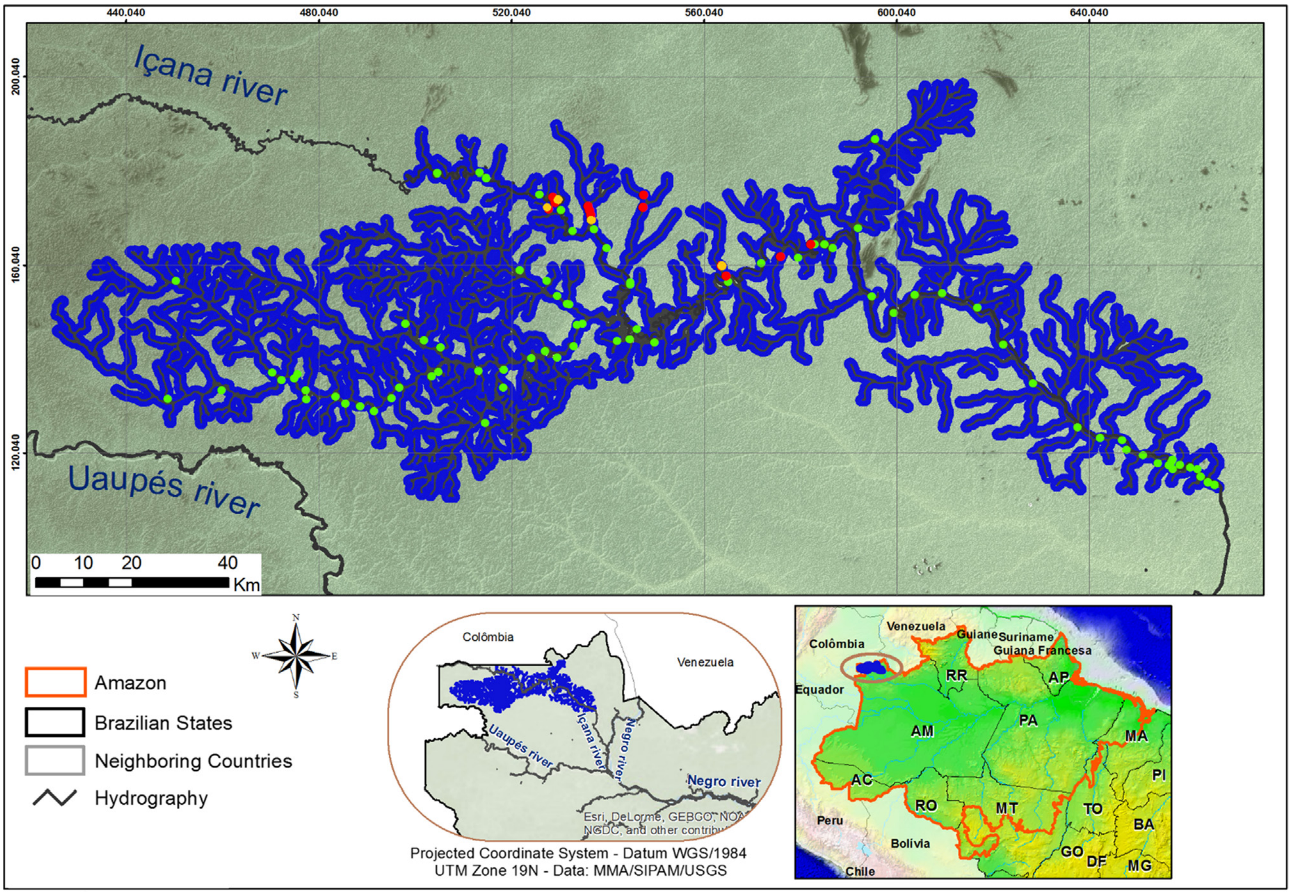

Fig. 3. Projection of the relative abundance of managed species in the Baniwa ancestral territory. Red dots represent plots sampled in ancestral forests (N = 12) and yellow dots in old-growth forests (N = 4). Green dots represent current Baniwa communities (Source: Instituto Socioambiental – ISA, unpublished data). According to our model, terra firme mature forests (closed-canopy forests) located ≤750 m from watercourses (buffer represented by the blue areas) have a mean abundance of approximately 15% of managed species. The mean abundance of managed species in ancestral forests was 21. 5% (max. 57%, mín. 5.4%) and in old-growth forests was 7.9% (max. 10.9%, min. 2.1%). The unweighted arithmetic mean ((21.5 + 7.9)/2) was 14.7% (rounded to 15% for purposes of discussion in the text), assuming that the region contains a proportional mosaic of ancestral and old-growth forests; our research suggests that old-growth forests are rare in the region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

abundant species in surveys of forest plots across the Amazon basin are considered to be incipiently domesticated species (ter Steege et al., 2013; Levis et al., 2017); moreover, 5 of the 14 species managed by the Baniwa in the current study are considered by the same authors to be incipiently domesticated (Levis et al., 2017).

Hyperdominant species with domesticated populations are more geographically widespread in Amazonia than non-domesticated hyperdominant species; most of the domesticated hyperdominants are found with incipiently, rather than fully domesticated populations (Levis et al., 2017; see also Clement, 1999 for definitions of the domestication process). Thus, ancient peoples of the Amazon appear to have managed incipiently domesticated species in standing forests rather than investing in full domestication of these populations and landscapes. Certainly, other factors, such as dispersal and pollination by animals, also contribute to species abundance in tropical forests (Wunderle, 1997; van Dulmen, 2001); however, the high abundance of domesticated and managed species clearly reflects a significant legacy of human activities on species abundance and forest structure in Amazonia (Erickson and Balée, 2006; Levis et al., 2017; Watling et al., 2017; Maezumi et al., 2018). Archaeobotanical research, including phytolith and palynological studies, could help refine our understanding of floristic changes through time (Mayle and Iriarte, 2014). Palynological studies, however, would be difficult in our study region since pollen requires special conditions for preservation (i.e., anaerobic lake bottoms and swamps; Pearsall, 2016) rarely present in this region.

Ancestral forests did not show a different mean value for total basal area when compared to old-growth forests (Fig. B5C), but their soils have more charcoal and lower acidity (Fig. 4 and Fig. B8A). We suggest that past Baniwa management in ancestral forests reduced soil acidity through periodic small-scale burning, as suggested by Denevan (2001) for other Amazonian areas, and as we observed in modern Baniwa communities. Basal area is a predictor of tree/palm biomass (Lima et al., 2012) and forest maturity (Saldarriaga et al., 1988) in the upper Negro River basin. Biomass resilience in Neotropical forests varies widely (Poorter et al., 2016); for the upper Negro River region, it has been estimated that after 190 years, deforested areas attain the biomass and basal area of mature forests, the latter calculated at 34.8 $m^2 ha^{-1}$ (Saldarriaga et al., 1988). We calculated an almost identical value for old-growth forests (35.1 $m^2 ha^{-1}$) and a higher value for ancestral forests (41.4 $m^2 ha^{-1}$; although the difference was not significant). Reduced soil acidity and the presence of high-biomass managed species, like *Poraqueiba sericea* and *Pouteria ucuqui*, probably contributed to the equivalent (and trending towards greater) biomass accumulation in ancestral forests when compared with old-growth forests. Thus, basal area data confirms our initial estimate (based on Baniwa oral histories and historical documents; Section 3.1) that ancestral forests have a minimum age of ~200 years (as well as old-growth forests), while suggesting that human management has contributed to an increase of forest biomass in the region. It is possible, nonetheless, that human management of these forests extends back to more ancient times.

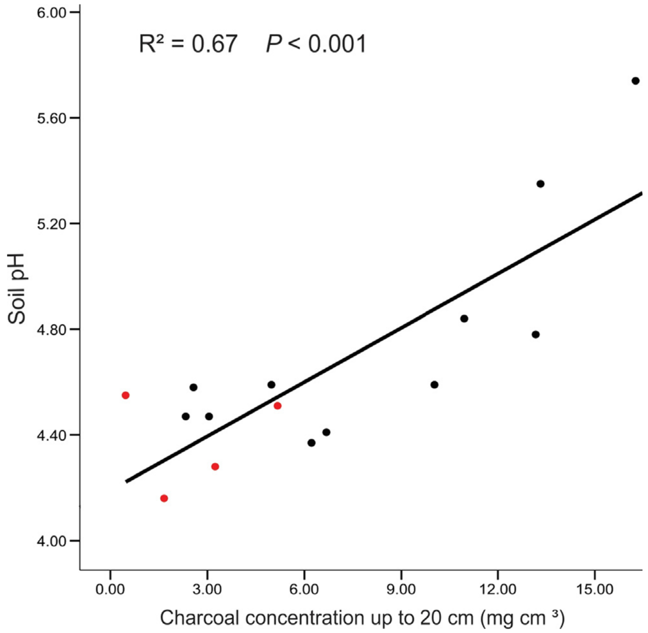

Fig. 4. Soil pH in relation to the charcoal concentration in soil (0–20 cm). Black dots represent plots in ancestral forests and red dots in old-growth forests. The black line is the simple linear regression *soil pH = 4.19 + 0.068 * charcoal concentration* ($R^2 = 0.67$; $P < 0.001$). N = 15 (one plot in ancestral forests was not included because the charcoal was damaged). Charcoal concentrations and soil pH in 0–20 cm layer were higher in ancestral forests (Fig. 4 and Fig. B8A). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

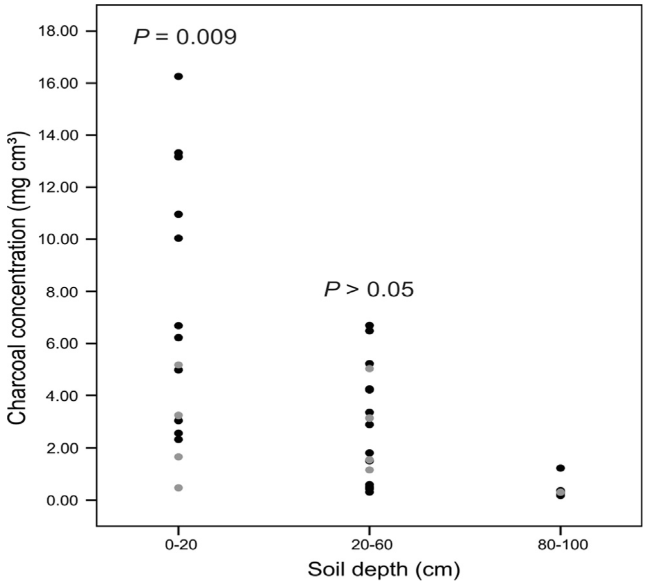

Fig. 5. Charcoal concentration in the soil at different depths in ancestral and old-growth forests. Black dots represent samples located in ancestral forests and grey dots in old-growth forests. In the 0–20 cm layer, N = 11 in ancestral forests and N = 4 in old-growth forests (Student's t teste, $P = 0.009$); in the 20–60 cm layer, N = 13 and N = 4, respectively (Student's t teste, $P > 0.05$); in the 80–100 cm layer, N = 6 and N = 1, respectively. Two plots located in ancestral forests were not included in the 0–20 and 20–60 cm analyses because the charcoal was damaged. Two extra samples of charcoal were included in the analysis of the 20–60 cm layer from ancestral forests that were not botanically inventoried.

Archaeological research in the upper Negro River region is still scarce, but prominent studies have shown that human occupation, including possible Arawak presence, dates back 4000–6000 years (Oliver, 1989).

Old-growth forests are considered "immemorial" forests to the Baniwa in terms of occupation and management. These forests are not necessarily "pristine": rather, no living Baniwa has any knowledge of past occupations there. However, in contrast to ancestral forests, we found no evidence of archaeological or other human artifacts on the soil surface of any of the old-growth forests surveyed. Archaeological excavation would be required to determine if these forests show signs of more ancient human occupation. The average abundance of managed species found in old-growth forests (7.7%) may reflect either the natural distribution of these species, or a more ancient legacy of human management that is gradually disappearing. Nonetheless, old-growth forests represent an adequate control group for our comparative study, because they represent the closest thing to "pristine" forests that we could locate within the study area.

According to our predictive model, about 15% of trees and palms in terra firme mature forests of the Içana basin within 750 m of all watercourses should be species managed by the Baniwa (Fig. 3), a direct reflection of the lasting human impacts on abundance of species throughout some ~15,000 km^2 of our study area. However, as our model focuses on closed-canopy, mature terra firme forests, it does not exclude the existence of other sorts of landscape in the same area such as younger secondary forests, igapó forests and current settlements and swiddens. Our results highlight the importance of ecological, ethnographic, ethnohistorical and ethnobotanical – and, additionally, archaeological – methods in research on landscape domestication in Amazonia. For example, recent modeling of the abundance of domesticated tree and palm species in Amazonian forests, based on the presence of archaeological sites (Levis et al., 2017), underestimates the degree of landscape domestication for our study region (the authors predict ~6% of relative abundance of domesticated species for the region), when compared with our results (~15% of relative abundance of managed species).

The dense network of medium and small streams in the region allowed the Baniwa to extend their forest management strategies far beyond the banks of the main rivers and tributaries. To date, models of precolonial anthropogenic effects in Amazonian forests have focused on the role of major navigable rivers in facilitating human management, while assuming negligible impacts in interfluvial areas due to their "less-fertile soils" and "poorer-quality resources" (McMichael et al., 2012, 2017; Bush et al., 2015; Piperno et al., 2015). Our model calls attention to the importance of smaller watercourses, and not only major "navigable" rivers, in facilitating human impacts in Amazonian forests. Streams adjacent to the two northernmost ancestral forests in Fig. 3 are only 3–5 m wide, and streams near other inventoried plots (ancestral and old-growth forests) vary from 3 to 8 m wide. These are not major watercourses by any definition, and fall into what are typically referred to as "*igarapés*" in Amazonia, a Tupi name that means literally "the way of the canoe". Indeed, the Baniwa constantly use their small canoes along *igarapés* to move through their territory. Interfluvial regions, therefore, include a dendritic network of "*igarapés*", as well as other wetlands (Junk et al., 2011), that have provided additional resources and facilitated indigenous management and occupation in Amazonia for millennia. Despite environmental limitations posed by nutrient-poor black water rivers and acidic, sandy soils, the Baniwa left a clear, lasting cultural legacy in ancestral forests, thus proving that "river bluffs" were not essential to past Amazonian livelihoods as some authors have suggested (McMichael et al., 2012, 2017; Bush et al., 2015; Piperno et al., 2015). Aquatic resources are of course essential to Amazonian livelihoods (Neves, 2007; Moraes, 2015), however "igarapés" are also able to provide them to some degree.

Another important human footprint left by landscape domestication is charcoal in the soil. In Amazonia, soil charcoal is common and its occurrence in savannas and ecotonal areas is often attributed to natural fires, especially during dry times such as the mid-Holocene drought episodes between 8000 and 4000 B.P. (Mayle and Power, 2008). Thus, soil charcoal does not necessarily indicate ancient human occupation in the area. In northwestern Amazonia, for example, areas of stunted forests – the *campina* or sandy savannas of the Içana basin – are subject to natural fires due to their open canopies and the large quantity of fuel (Kauffman et al., 1988). However, closed-canopy forests in northwestern Amazonia – the "terra firme" or *campinarana* of the Içana basin – do not usually burn without human intervention due to their high relative humidity (> 65%) (Uhl et al., 1988). In moist Amazonian forests more generally, natural fires are rare (Cochrane, 1999; Mayle and Power, 2008). Although dry climatic phases are registered in some parts of Amazonia (Wijmstra and Van der Hammen, 1966; Van der Hammen, 1972, 1982; Absy, 1985), in northwestern Amazonia there is no signal of interrupted forest cover in closed-canopy forests in the last few millennia (Colinvaux et al., 1996; Bush et al., 2004), suggesting that forest humidity remained very similar to what it is today, especially over the past ~4.000 years when precipitation regimes have remained stable (van Breukelen et al., 2008). Therefore, paleoecological data reinforce our results and suggest that charcoal records in our forest plots, especially in old-growth forests, do not have a natural, but rather an anthropogenic origin.

The oldest records of human occupation in the upper Negro River basin date back to 3570 (Neves, 1998) and 3750 (Sanford et al., 1985) years B.P., and both dates were recorded less than 150 km from our study region. Charcoal samples in an area less than 150 km from our study site, likewise dominated by closed-canopy forest with similar floristic structure and composition, dated to between 250 and 640 years B.P. for the top 20 cm soil layers and between 530 and 6260 years B.P. for the lower 20–90 cm soil layers (Saldarriaga and West, 1986). Models relying on archaeological and linguistic evidence suggest human occupation by ~6000 B.P in northwestern Amazonia (Oliver, 1989). Given the long history of human occupation in northwestern Amazonia, the universal presence of higher charcoal concentrations in the top 20 cm of soil in historical Baniwa settlements abandoned in the past few centuries, and the lower charcoal concentrations in the top soil layer at sites where the Baniwa do not recognize historical settlements, we infer a greater intensity of burning (presumed to be related to swiddens and agroforestry; see Denevan, 2001; Maezumi et al., 2018) in ancestral forests when compared with old-growth forests over the past few centuries, with similar intensities in earlier times. In sum, the observed differences in floristic structure and abundance of species between ancestral and old-growth forests appear related to management by ancestral Baniwa populations during the last few centuries, although these landscapes may have been managed for even longer.

Additional archaeological and archaeobotanical studies will be required to understand the time depth of human occupation and the extent of landscape domestication in this region. More generally, further research will be required to investigate the extent of landscape domestication in other interfluvial areas across Amazonia. Even "everwet" forests such as found in our study area, considered "natural" (Bush et al., 2015) and with minimal historical human influence (McMichael et al., 2015, 2017), may bear the legacy of ancient human alterations and management. The only way to distinguish ancestral forests modified by past human actions from pristine or natural forests, untouched by human agency, is through interdisciplinary research combining floristic sampling with soil analysis, ethnography, oral histories of past human occupation, and at least surface surveys for artifacts, or ideally more in-depth archaeological work (Chazdon, 2012). As a result, processes of landscape domestication, such as those documented here, may be found to be more widespread than is currently believed.

Contemporary anthropological theory, drawing largely on the analysis of myth and cosmology, has emphasized the fluidity between the categories of "nature" and "culture" for Amazonian indigenous peoples (Descola, 1996; Viveiros de Castro, 1998; Cabral-Oliveira, 2016). This study confirms how the socio-environmental practices of Amazonian peoples give rise to mature forest environments that are as much the product of cultural as of natural forces. The processes that create cultural forests also run the other way, creating a kind of "forested" human culture, manifest in the striking salience of biodiversity and ecological concepts in Amazonian myth and cosmology (Reichel-Dolmatoff, 1976; Århem, 1996). By the same token, large swathes of Amazonia, previously thought by scientists to be "natural" and untouched by humans, may turn out to be fundamentally social spaces, domesticated by humans for human ends, and yet without excluding the multitude of other species and ecological processes that continue to make the region crucial to conservation and global climate stability.

Nonetheless, from 2015 to 2018, deforestation has increased in Amazonia, and about 20% of the forest cover is already gone (Artaxo, 2019). Recent models suggest that the tipping point for irreversible transformation into savanna could be 25% overall deforestation (Lovejoy and Nobre, 2018). Projecting current trends of agricultural expansion, 40% of Amazonian forests will no longer be standing by 2050 (Soares-Filho et al., 2006). Although their role in biodiversity conservation has been questioned (Robinson, 1993; Redford and Sanderson, 2000; Terborgh and Peres, 2002; Barlow et al., 2012), indigenous and other Amazonian traditional peoples are increasingly seen as key allies in defending forest cover (Soares-Filho et al., 2010; Blackman et al., 2017), managing resources (Chapin, 2004; Stevens et al., 2014), and preventing species extinctions into the future (ter Steege et al., 2015). Indigenous lands include more than one-quarter of Brazilian Amazonian forests (IPAM, 2015) and represent large islands of standing forests serving as effective barriers against deforestation (RAISG et al., 2017). Nonetheless, indigenous rights suffered a sharp blow in the 2018 federal elections in Brazil. Legislation currently under debate in the Brazilian congress (PL 1610/1996) threatens to weaken indigenous peoples' constitutionally guaranteed territorial rights and open their lands to mining and other economic interests (Ferreira et al., 2014; Fearnside, 2016) and free up commercial farming (Artaxo, 2019; The Guardian, 2019). A total of 387 requests for mining concessions are currently pending for the upper Negro River Indigenous Territory where this study was carried out (Almeida et al., 2016). If granted, this legislation would expose ancestral and old-growth forests to deforestation, fragmentation and water pollution (Bizri et al., 2016; Sonter et al., 2017), besides putting at risk the livelihood of the Baniwa and other indigenous people of the region.

We call for a reconsideration of biodiversity conservation policies and indigenous rights in Amazonia. Although the Brazilian constitution recognizes that indigenous people have rights to their traditional territories, it is important that domesticated landscapes are recognized as signatures of their traditional occupation. In this sense, indigenous people can be seen as "co-authors" of the current biodiversity inside their territories. If large portions of forests are not "virgin" or "natural", but are rather partly domesticated by their ancestral indigenous inhabitants (Clement et al., 2015; Levis et al., 2017; Maezumi et al., 2018), it stands to reason that ongoing protection of these landscapes should contemplate the role indigenous people in their formation and historical/ongoing management. Moreover, understanding how indigenous people domesticated tropical forest landscapes in the past and into the present (Levis et al., 2018) provides an important scientific background for contemporary forest management and long-term socio-environmental resilience (Mulyoutami et al., 2009; Wangpakapattanawong et al., 2010). Conservation strategies and public policies should respect indigenous peoples' rights and recognize their historical role in managing Amazonian forests sustainably for millennia.

Author contributions

J.F.M., C.R.C. and G.H.S. conceived of the project; J.F.M. collected field data and carried out laboratory analyses; G.H.S. made a follow-up field visit with J.F.M in 2018 to return results to the study communities and observe ongoing processes of Baniwa management (see Appendix A); A.F.M.B.B. accompanied all phases of field research, translated and facilitated community contacts, and participated in site selection and identification; J.F.M. and F.R.C.C. analyzed the data; H.P.L. contributed to the literature review and contextualization of the results as they relate to the archaeological record; J.F.M. wrote the initial draft; J.F.M., F.R.C.C., H.P.L., C.R.C. and G.H.S. revised successive drafts.

Acknowledgements

We thank the Baniwa communities of Bobope (Bela Vista), Ttdzealinomana (Santa Marta), Hizdapada (Mauá Cachoeira), Komalhipani (Tucumã Rupitá) and Owhika (Santa Rosa) for their hospitality and patience during field work; Natalia Camps Pimenta for pooling resources on joint field trips to the same region for independent projects; the Instituto Socioambiental for logistical support in São Gabriel da Cachoeira; the Federação das Organizações Indígenas do Rio Negro and the Organização Indígena da Bacia do Içana for authorizing the study and providing assistance when necessary; the Baniwa field assistants André, Armando (*in memoriam*), Carlos, Charles, Francisco (*in memoriam*), Gerunso, Gilberto, Januário, Názário, Paulo Filho, Pedro, Plínio, Samuel, and Wilson; Laura Oliveira of INPA's Thematic Laboratory of Plants and Soils for assistance with soil analyses; Bruce Nelson, INPA, and André Arruda, Greenpeace, for assistance and elaboration of maps, respectively; and the Conselho Nacional de Desenvolvimento Científico and Tecnológico (CNPq) for a Master's scholarship to J.F.M. and research fellowships for H.P.L., F.R.C.C., C.R.C. and G.H.S.

Funding

Field work was funded by National Geographic Society grant 9785-15.

Appendix A–C. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.04.020.

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