











RESEARCH PAPER

Legacy of Amazonian Dark Earth soils on forest structure and species composition

Edmar Almeida de Oliveira¹  | Ben Hur Marimon-Junior¹  |
 Beatriz Schwantes Marimon¹  | José Iriarte²  | Paulo S. Morandi¹  |
 S. Yoshi Maezumi^{2,3}  | Denis S. Nogueira⁴  | Luiz E. O .C. Aragão^{5,6}  |
 Izaias Brasil da Silva⁷  | Ted R. Feldpausch^{1,5} 

¹Programa de Pós-Graduação em Biodiversidade e Biotecnologia da Rede BIONORTE, Universidade do Estado de Mato Grosso – UNEMAT, Nova Xavantina, Mato Grosso, Brazil

²Archaeology, College of Humanities, University of Exeter, Exeter, UK

³Ecosystem and Landscape Dynamics/ Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, the Netherlands

⁴Instituto Federal de Mato Grosso, Primavera do Leste, Mato Grosso, Brazil

⁵Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

⁶Divisão de Sensoriamento Remoto, Instituto Nacional de Pesquisas Espaciais-INPE, São José dos Campos, São Paulo, Brazil

⁷Programa de Pós-Graduação em Biodiversidade e Biotecnologia da Rede BIONORTE, Universidade Federal do Acre-UFAC, Rio Branco, Acre, Brazil

Correspondence

Edmar Almeida de Oliveira and Ben Hur Marimon-Junior, Programa de Pós-Graduação em Biodiversidade e Biotecnologia da Rede BIONORTE, Universidade do Estado de Mato Grosso – UNEMAT, *Campus* de Nova Xavantina, BR 158, km 655, P.O. Box 08, 78690-000, Nova Xavantina, Mato Grosso, Brazil.
 Emails: edmardinei@gmail.com; bhmarimon@unemat.br

Ted R. Feldpausch, Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4RJ, UK.
 Email: T.R.Feldpausch@exeter.ac.uk

Abstract

Aim: Amazonian forests predominantly grow on highly weathered and nutrient poor soils. Anthropogenically enriched Amazonian Dark Earths (ADE), traditionally known as *Terra Preta de Índio*, were formed by pre-Columbian populations. ADE soils are characterized by increased fertility and have continued to be exploited following European colonization. Here, we evaluated the legacy of land-use and soil enrichment on the composition and structure in ADE and non-ADE (NDE) forests.

Location: Eastern and southern Amazonia.

Time period: Pre-Columbia – 2014.

Methods: We sampled nine pairs of ADE and adjacent NDE forest plots in eastern and southern Amazonia. In each plot, we collected soil samples at 0–10 and 10–20 cm depth and measured stem diameter, height, and identified all individual woody plants (palms, trees and lianas) with diameter ≥ 10 cm. We compared soil physicochemical properties, vegetation diversity, floristic composition, aboveground biomass, and percentage of useful species.

Results: In the nine paired plots, soil fertility was significantly higher in ADE soil. We sampled 4,191 individual woody plants representing 404 species and 65 families. The floristic composition of ADE and NDE forests differed significantly at both local and regional levels. In southern Amazonia, ADE forests had, on average, higher aboveground biomass than other forests of the region, while in eastern Amazonia, biomass was similar to that of NDE forests. Species richness of both forest types did not differ and was within the range of existing regional studies. The differences in composition between large and small diameter tree recruits may indicate long-term recovery and residual effects from historical land-use. Additionally, the proportion of edible species tended to be higher in the ADE forests of eastern and southern Amazonia.

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Main conclusions: The marked differences in soil fertility, floristic composition and aboveground biomass between ADE and NDE forests are consistent with a small-scale long-term land-use legacy and a regional increase in tree diversity.

KEYWORDS

anthropogenic, archaeology, conservation, ethnobotany, palaeoecology, Palaeoindian, pre-Columbian

1 | INTRODUCTION

The degree to which pre-Columbian people modified Amazonia is one of the most debated topics in ecology, botany, archaeology, palaeoecology, soil science and conservation (Balée, 2013; Barlow, Gardner, Lees, Parry, & Peres, 2012; Clement et al., 2015; Glaser, Balashov, Haumaier, Guggenberger, & Zech, 2000; Heckenberger et al., 2008; Lehmann, Kern, Glaser, & Woods, 2003; Levis et al., 2017; McMichael, Feeley, Dick, Piperno, & Bush, 2017; McMichael, Matthews-Bird, Farfan-Rios, & Feeley, 2017; McMichael et al., 2012; Schaan et al., 2012; Willis, Gillson, & Brncic, 2004; Woods et al., 2009). Recent work conducted across the Amazon Basin also suggests potential landscape-scale legacies contributing to the floristic composition and diversity of modern forests (Levis et al., 2017). A disproportionate number of plants are hyperdominant (ter Steege et al., 2013) and domesticated species are five times more likely to be hyperdominant than non-domesticated species (Levis et al., 2017). These data suggest that modern forest composition was influenced by past populations. However, it is unclear to what extent the pre- and post-Columbian peoples may have affected the observed floristic patterns and structure of modern Amazon forests (McMichael et al., 2017).

One of the most compelling lines of evidence for widespread anthropogenic influence comes from the presence of the anthropogenically made Amazonian Dark Earth (ADE) soils (Glaser et al., 2000; Lehmann et al., 2003; Woods et al., 2009). Previous studies from the eastern Amazon have shown that pre-Columbian crop cultivation and agroforestry altered the modern composition, enriching modern ADE forests in edible plant species (Maezumi et al., 2018).

Following the arrival of European colonialists in the 15th and 16th centuries, the pre-Columbian populations were estimated in the millions (Nevle, Bird, Ruddiman, & Dull, 2011). This population rapidly declined by up to 90% due to introduced diseases, with entire civilizations permanently lost, leaving behind the legacy of enriched ADE soils (Koch, Brierley, Maslin, & Lewis, 2019; Nevle et al., 2011).

Today, ADEs continue to be used by local farmers for planting, given their high fertility (Clement, McCann, & Smith, 2003). ADEs are formed from the anthropic addition of organic matter, household wastes, ceramics, and charcoal (Sombroek et al., 2002). Organic matter and nutrients from household waste are retained in the soil through chemical-physical interactions with pyrogenic carbon, which enhances soil fertility (Kämpf, Woods, Sombroek, Kern, & Cunha, 2003; Lehmann, Pereira da Silva, et al., 2003). This effect is due to the properties of macro- and microscopic pyrolysed carbon formed from incomplete combustion of biomass during burning (Glaser, Haumaier, Guggenberger, & Zech, 2001). This fertilization process contributes to the soil retention/availability of water and nutrients, conferring advantages for agriculture (César et al., 2011) and native forest productivity (Aragão et al., 2009) over Amazonian dystrophic soil types, such as nutrient poor latosols.

As a result of the anthropogenic enrichment of ADE soils, the forests growing on abandoned ADEs may be characterized by different growth and structure (Aragão et al. 2009), such as lower and more closed canopies and more understorey trees (Sombroek et al., 2002). ADE forests also allocate more carbon to plant biomass gain than non-ADE (NDE) soils (Doughty et al., 2013). ADE sites can therefore be considered a long-term fertilization experiment to test legacy effects on current native vegetation of landscape management

by ancient human populations (Cook-Patton, Weller, Rick, & Parker, 2014). To date, there is little information to determine which species occur in these environments at a broader scale or whether ADEs can accumulate more species due to their stability, productivity and fertility (Aragão et al., 2009; Cunha et al., 2007; Glaser et al., 2000). Diameter distributions can reveal patterns of tree species dynamics, e.g., whether a forest is recovering from disturbance (Lima, Bufalino, Alves Júnior, Silva, & Ferreira, 2017), and can be an important tool to detect some legacy of old land-use in forest structure, for the ADEs' land-use legacy can remain recorded in the structure of present-day forests (Junqueira, Shepard, & Clement, 2011; Woods & McCann, 1999).

Additionally, the edaphic changes associated with ADE soils that increase fertility and water retention can create distinct habitats that persist for centuries after abandonment (Glaser et al., 2001). Some studies suggest that forests growing on ADEs can be compositionally and structurally distinct from surrounding vegetation (Clement et al., 2009; Junqueira, Shepard, & Clement, 2010; Palace et al., 2017) and may contribute to the diverse and heterogeneous tree flora of Amazonia (Aragão et al., 2009; Sombroek, 1966). To date, understanding the mechanisms that determine the composition, structure and diversity of Amazonia forests is a major challenge (Bicudo, Sacek, Almeida, Bates, & Ribas, 2019; Hoorn et al., 2010; Levis et al., 2017). While studies have suggested the importance of past land-use as a factor in increasing the diversity and distribution of current species (Cook-Patton et al., 2014; Levis et al., 2017), it is unclear whether edaphic factors associated with ADE soils also influence species richness in Amazonia.

The aim of this study was to evaluate the potential legacy of ADEs and their contribution to the structure and floristic composition of modern forests with the following questions: (a) Do forests that grow on ADEs have different richness and floristic composition than adjacent forests? (b) Does forest structure and aboveground biomass differ between ADEs and NDEs? (c) Is the diversity of edible species in ADE forests greater than in NDE forests? Our study takes a novel approach by studying ADE and NDE forests in two distant regions, with contrasting environments and occupation history, to evaluate whether differences between ADE and NDE forests that were already identified in local studies are consistent across broader scales. We also focus on mature forests growing on ADEs, which are less studied than secondary forests or agroecosystems growing on ADEs.

2 | MATERIAL AND METHODS

2.1 | Study area

We carried out the study in forests growing on ADEs and NDEs in southern (S) and eastern (E) Amazonia, in the states of Mato Grosso and Pará, Brazil. In southern Amazonia, Cerrado-Amazonia forest zone of transition, we sampled three ADE forests (ADE-S-01, 02 and 03) and three NDE forests (NDE-S-01, 02 and 03) within

the municipalities of Ribeirão Cascalheira, Gaúcha do Norte and Querência, all in the state of Mato Grosso. In eastern Amazonia, we sampled six ADE forests (ADE-E-01, 02, 03, 04, 05 and 06) and six NDE forests (NDE-E-01, 02, 03, 04, 05 and 06) in the FLONA reserve (Tapajós National Forest), municipality of Belterra, state of Pará (Figure 1; Supporting Information Table S1).

The forests in southern Amazonia are seasonal evergreen, a forest type found in seasonal climates with a dry season longer than 120 days (Ivanauskas, Monteiro, & Rodrigues, 2008). These forests have little leaf loss during the dry season, which differs from the semi-deciduous or deciduous seasonal forests of eastern Brazil (Oliveira-Filho & Ratter, 1995). The forests of eastern Amazonia are classified as *terra firme* dense rain forest (IBAMA, 2004, sensu RADAMBRASIL, 1982). This phytophysiognomic type represents most vegetation of northern Brazil and is characterized by a closed canopy, large individual trees, and high temperature and humidity (Velooso, Rangel-Filho, & Lima, 1991).

Southern Amazonian sites have two well-defined seasons with a dry season from April to September and a rainy season from October to March. Eastern Amazonian sites have a dry season from July to October and wet season from November to June. The average annual rainfall is 1,613 mm in Gaúcha do Norte municipality (Mato Grosso state) and 1,997 mm in Belterra (Pará state). The average annual temperature varies between 24.1 and 25.5 °C (Supporting Information Table S1). All climatic variables were extracted from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

Some regions of Pará and Mato Grosso have a long history of pre-Columbian occupation. In the Xingu River region (Mato Grosso state), dozens of pre-Columbian settlements have been documented, fortified by ditches and connected by a regional network of roads in a 'galactic' system of regional polities extending over 20,000 km² that peaked around c. 750–500 cal BP (Heckenberger et al., 2008). The Santarem region (Pará state) has one of the earliest occupation histories in Amazonia, with archaeological evidence of Palaeoindian occupation of Pedra Pintada Cave (c. 13,000 cal BP; Roosevelt et al., 1996). Later Archaic occupations in the region are represented by the Taperinha shell-midden, which contains the earliest ceramics in Amazonia (c. 7,900 cal BP; Roosevelt, Housley, Silveira, Maranca, & Johnson, 1991). The Formative Period occurred between c. 4,500 and 1,000 cal BP (Gomes, 2011) followed by the Late pre-Columbian Tapajó Period (LPTP) from c. 1,000 to 400 cal BP (Stenborg, Schaan, & Amaral-Lima, 2012). The LPTP exhibits extensive landscape modifications including the development of ADE sites, a network of ditch and causeway trails connecting sites, and numerous water collecting pools constituted by natural pools that have been artificially enhanced as reservoirs. Archaeological investigations in one of our study regions, the Tapajós National Forest (FLONA Tapajós), show indications of human occupation since at least 4,500 yr BP and the development of ADEs in this region occurred between c. 530 and 450 cal BP corresponding to the phase of the LPTP (Alves, 2018; Maezumi et al., 2018).

ADE patch size in Amazon varies from less than one hectare to several hundred hectares, with most of the recorded sites < 2 ha (Kern

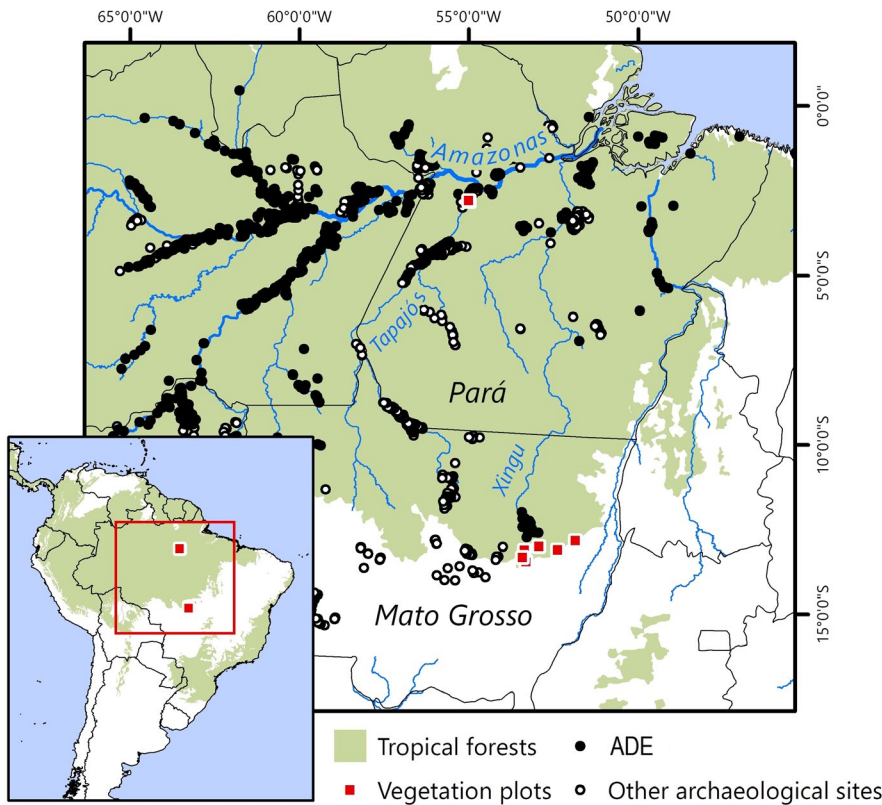


FIGURE 1 Plot locations in forests in southern Amazonia represented by the state of Mato Grosso (MT) and eastern Amazonia represented by the state of Pará (PA), Brazil. The black line in the inset indicates the boundaries of Brazilian states. The areas in Pará overlap and, due to their proximity, they are represented as a single dot. Archaeological sites - ADE (Amazonian Dark Earth) data sourced from the National Register of Archaeological Sites (CNSA) (IPHAN, 2018)

et al., 2003). ADEs are estimated to cover c. .1–.3% (6,000–18,000 km²) of the forested portion of the Amazon Basin (Woods & Denevan, 2009), although the predictive model used by McMichael et al. (2014) estimated that ADEs may cover as much as 3.2% (approximately 154,063 km²). ADEs are generally found along major rivers, and in certain regions, such as Santarém (Schaan, 2012) and on the middle Purus and Madeira Rivers (Levis et al., 2012), are also found in interfluvial areas. In the central and lower portion of Amazonia, ADE formation began around or after 2,000 cal BP (Arroyo-Kalin, 2010; Heckenberger & Neves, 2009; Maezumi et al., 2018), although ADEs appear to be older in the Upper Madeira River (Miller, 1992). After the Columbian Encounter around 500 cal BP, indigenous populations began to decline (Denevan, 1992) and indigenous land-use on ADEs was largely abandoned.

2.2 | Data collection

2.2.1 | Experimental design

In the southern Amazonian (S) sites, we set up three pairs of 1 ha plots (100 m × 100 m): three in ADE and three in NDE. In the eastern Amazonian (E) sites, we set up six pairs of .25 ha plots (50 m × 50 m). Due to the current use of ADE by local populations, we reduced plot size to allocate to the most preserved forest patches. The NDE plots were established at least 150 m from ADEs in soils without traces of ceramic artifacts and charcoal. The southern Amazonian sites were isolated until recent large-scale farms were established and prior post-colonial land-use was unlikely (Vilas-Bôas & Vilas-Bôas, 2012).

2.2.2 | Soil sampling and analyses

ADE soils were characterized according to Lehmann, Kern, et al. (2003), being recognized for the high amount of pyrogenic carbon (charcoal, incompletely burned organic matter) and archaeological artifacts, mainly shards of ceramic and lithic material found in soil pits (Costa, Kern, Pinto, & Souza, 2004; Denevan, 1992; Glaser et al., 2001; Kern et al., 2003). In each 100 m × 100 m plot in southern Amazonia, we collected soil samples at 0–10 and 10–20 cm depth from five random points. In the 50 m × 50 m plots of eastern Amazonia, we collected a single soil sample at 0–10 and 10–20 cm depth at the centre of each plot. Samples were air-dried at ambient temperature and analysed for physical (clay, silt and sand) and chemical properties [pH(H₂O), P, K, Ca, Mg and Al], and sum of bases (SB, cmolc/dm³), organic matter (OM, g/dm³), cation exchange capacity (CEC, cmolc/dm³) and the ratios Ca:Mg, Al³ + H:CEC (%), Ca:CEC (%) and Mg:CEC (%) (Supporting Information Table S2) using standard protocols (F. C. Silva, Eira, Barreto, Pérez, & Silva, 1998).

2.2.3 | Vegetation sampling, biomass estimates, useful species

In each study plot, we sampled all live woody plants (including palms, trees and lianas) with diameter (D) ≥ 10 cm at breast height (1.3 m) and measured their heights with a Leica (Heerbrugg, Switzerland) DISTO™D5 laser measurement device. The lianas were measured at 1.3 m

along the stem. We identified species in the field and when necessary collected vouchers for confirmation by specialists. The material was deposited in the NX Herbarium, Nova Xavantina, Mato Grosso State. We determined the aboveground biomass (B) of each tree based on a pantropical model (Chave et al., 2005) $B = .0509 \times (\rho D^2 H)$; where D is individual diameter (cm) at 130 cm height or above deformities and buttress roots, H is total tree height (m), and ρ is wood density (g/cm^3) compiled from the DRYAD global database (Chave et al., 2009; Zanne et al., 2009) and summed biomass per hectare (Mg ha^{-1}). Where individual tree height estimates were lacking, we estimated tree height using the pantropical allometric equation [$H = a(1 - \exp(-b D^c))$] by Feldpausch et al. (2012), where the coefficients a , b and c were determined for each region (e.g., eastern/central and southern Amazonia)]. These equations together minimize the error in biomass estimation [Feldpausch et al. (2011) and Feldpausch (2012)].

We classified tree species as 'useful species' (medicinal, food, construction, and fibre) and edible based on the literature (Clement, 1999; Junqueira et al., 2010, 2011; Levis et al., 2017, 2012; López Zent & Zent, 1998; Maezumi et al., 2018; Prance, Balée, Boom, & Carneiro, 1987). Due to the lack of information on which species indigenous people previously used in the Cerrado-Amazonia forest zone of transition, we used the same classification for useful species for both southern and eastern Amazonian sites.

2.3 | Statistical analysis

To evaluate the physicochemical properties of the ADE and NDE soils in the two regions, including grain size (clay, silt and sand), chemical properties [pH(H_2O), P, K, Ca, Mg and Al], sum of bases, organic matter, cation exchange capacity, and the ratios Ca:Mg, $\text{Al}^3 + \text{H}:\text{CEC}$, Ca:CEC and Mg:CEC, we used a permutational multivariate analysis of variance (PerMANOVA) test with 1,000 randomizations (Anderson, 2001).

We assessed the sampling effort (rarefaction curves) based on the interpolation and extrapolation method in iNEXT (Chao et al., 2014; Hsieh, Ma, & Chao, 2016). This analysis enabled the calculation of the richness of samples by extrapolation of the plot abundance based on plot size. We compared local communities and estimated the richness of each area generating value for estimators incidence coverage-based estimator, abundance coverage-based estimator (ACE), Chao1 Chao2, Jackknife1 and Jackknife2, whose values were obtained from 1,000 randomizations in the program ESTIMATE S 8.0 (Colwell, 2008). The estimators were selected using abundance data following Hortal, Borges, and Gaspar (2006). These estimators infer the richness when plot size is unequal and/or small, e.g., Chao 1 and ACE are highly precise regarding variation in sample size. However, the most precise estimator was selected using the highest R^2 value from a regression analysis between the observed and estimated values (Brose, Martinez, & Williams, 2003).

We determined tree species diversity using the Shannon index (H') and evenness with the Hurlbert index (probability of interspecific

encounter, PIE), in the program EcoSIM 7.0 (Gotelli & Entsminger, 2001). To test whether the local diversity varied between ADE and NDE forests, we used a PerMANOVA (Anderson, 2001) based on 1,000 randomizations. We consider the estimated richness (S), Shannon index (H') and Hurlbert evenness index (PIE), highly dependent values, as a measure of local diversity. To minimize sampling bias, we determined the values estimated for S , H' and PIE using the rarefaction method (1,000 randomizations) in the program EcoSIM 7.0 (Gotelli & Entsminger, 2001), taking as reference the community with the lowest abundance.

We used one-way ANOVA to compare the total aboveground biomass between ADE and NDE forests at a local scale (southern and eastern Amazonia), and a t -test to compare the biomass between forest types (ADE versus NDE) regardless of the region (Legendre & Legendre, 1998). We tested the normality of residuals and homogeneity of variance with Shapiro-Wilk (mean = 209.1, $w = 0.92$, $p = .142$) and Levene tests [$F_{(1,3)} = 1.19$, $p = .352$], respectively.

To test the potential legacy effects of soil fertility on the vegetation composition and species abundance in ADE and NDE forests through time, we categorized stems into three diameter classes (10–20, > 20–40 and > 40 cm) and applied a Bray–Curtis dissimilarity index. This index includes presence and absence and the abundance of species in all diameter classes. We considered that those classes represented a chronological order in which individual trees in the class > 40 cm are the oldest in the forests. While larger diameter classes can contain fast-growing, young trees, we considered that on average the largest trees are the oldest in structurally intact forests and therefore serve as a metric of long-term legacy effects of soil modifications on forest composition. Therefore, comparisons of different classes, e.g., 10–20 cm versus > 40 cm, indicate whether forests are changing over time. In addition, we used the same diameter classes and applied the PerMANOVA test using the Bray–Curtis distance to test whether ADE forests are more similar to present (smallest diameter class) or past NDE forests (largest diameter class). Due to the small number of individual trees in the class > 40 cm in ADE and NDE forests of Pará (eastern Amazonia), we used the three plots together (totaling .75 ha).

We evaluated dissimilarities in floristic composition and species abundance in ADE and NDE forests using non-metric multidimensional scaling (NMDS; Legendre & Legendre, 1998). The sampling deficit (size of plots) can affect comparisons of richness and floristic composition between areas because the smaller plots harbour only a subset of the regional floristic composition and a reduced number of individuals (Chao & Jost, 2012). Thus, we calculated the dissimilarity expected for a rarefied community considering the smallest number of individuals sampled among all communities (53 living individuals) and applied the extended dissimilarities using an extended version (path = "extended") with the *vegan* package in the R program (R Development Core Team, 2018). The dissimilarity was also calculated with the Raup–Crick probabilistic estimator considering probability of occurrence greater than zero as presence and equal to zero as absence based on the rarefied matrix. The matrix was ordered using the meta MDS function of the *vegan*, a nonmetric

multidimensional scaling function with stable solutions from random starts, axis scaling and species scores (Oksanen et al., 2018). The result of the analyses showed little or no 'arc effect', while keeping the groupings of the sites homogeneously distributed within the different areas, congruent with the analysis based on the Bray–Curtis dissimilarity. Thus, we maintained NMDS based on the Bray–Curtis dissimilarity matrix.

Our general objective was to compare key abiotic (soil) and biotic (vegetation) attributes between ADEs and NDEs forests, including (a) soil; (b) vegetation richness, diversity and evenness; (c) aboveground biomass; (d) species composition and size classification; (e) useful and edible species. To gain further insights, we conducted these comparisons at two organizational scales: plot and region. Given that we conducted multiple comparisons using the same data, but organized at different scales, we used Bonferroni-adjusted p -values to take account of multiple tests of the PerMANOVA. We divided the level of significance adopted (.05) by the number of statistical tests performed (three) (Dunn, 1961). For these tests, we adopted a p -value of .0167. However, as the p -values were obtained based on randomization, we suggest using both approaches (original and Bonferroni-adjusted p -values).

All tests where a specific program was not stated were executed in R (R Development Core Team, 2018), with the *vegan* package (Oksanen et al., 2018).

3 | RESULTS

3.1 | Soil and vegetation patterns of ADEs

In general, ADE forests had significantly higher pH and fertility, with P, K, Ca, Mg (magnesium), OM, SB and CEC all higher than in NDE forests. Ca:Mg, Ca:CEC, Mg:CEC ratios were also higher in ADE forests. Only Al and the Al³ + H:CEC ratio were lower for this type of soil. The soils of eastern Amazonia had higher clay and silt content than the sandier soils of southern Amazonia (see Supporting Information Table S2 and the PerMANOVA results in Supporting Information Table S3).

We sampled a total of 4,191 individual trees of 404 species and 65 families: 3,035 individuals of 194 species and 47 families in southern Amazonia (S) and 1,156 individuals of 247 species and 53 families in eastern Amazonia (E). The families with the greatest distribution (present in all plots) and highest species richness included: Fabaceae, Annonaceae, Lauraceae, Burseraceae, Moraceae and Sapotaceae (Figure 2). The other families had a more restricted distribution (Supporting Information Table S4). The families Melastomataceae and Apocynaceae occurred only in NDE forests in both regions and Myrtaceae only in NDE-S forests. Malvaceae and Arecaceae were restricted to ADE-E and Bignoniaceae and Rubiaceae to ADE-S.

At the species level, 20 taxa showed a broad distribution among the ADE forests [among them *Apuleia leiocarpa* (Vogel) J.F. Macbr., *Guazuma ulmifolia* Lam., *Hymenaea courbaril* L., *Inga laurina* (Sw.)

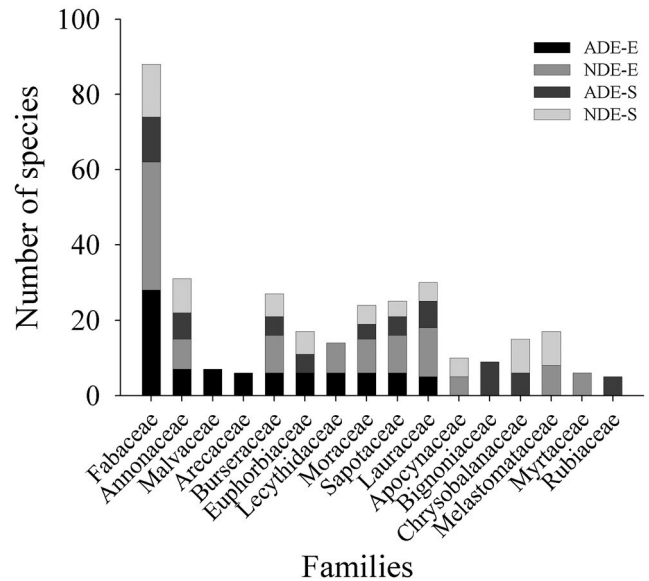


FIGURE 2 Number of species for each family sampled in Amazonian Dark Earth (ADE) and non-Dark Earth (NDE) forests located in eastern (NDE-E and ADE-E) and southern Amazonia (NDE-S and ADE-S)

Willd. and *Maclura tinctoria* (L.) D. Don ex Steud.] and 15 between the NDE forests, with the other species showing a local distribution. *Jacaranda copaia* (Aubl.) D. Don, *Hymenaea courbaril* L., *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin occurred in all forests in both regions (Supporting Information Table S4).

After accounting for sampling effort, we recorded a marked increase in rarefaction curves for ADE and NDE-E forests (Figure 3) and a moderate increase in ADE and NDE-S forests (Figure 3).

At regional scales, NDE forests showed similar richness (S), diversity (H') and evenness values (PIE) (ADE versus NDE, PerMANOVA, $F_{(1,17)} = 1.58$, $r^2 = .08$, $p = .22$) (species S , H' and PIE in Table 1) and higher aboveground biomass (mean = 256.18) than ADE forests (mean = 162.02) ($t = 2.39$, $df = 16$, $p = .03$).

At the local scale, richness (S), diversity (H') and evenness values (PIE) (alpha diversity) did not differ (ADE-S versus NDE-S, PerMANOVA, $F_{(1,5)} = 1.11$, $r^2 = .03$, $p = .90$ and ADE-E versus NDE-E, PerMANOVA, $F_{(1,11)} = 4.40$, $r^2 = .31$, $p = .06$, individual values shown in Supporting Information Table S5). However, there was larger variation in aboveground biomass values (Supporting Information Table S5): NDE-E showed, on average, higher values than NDE-S and ADE-E, and similar values to ADE-S forests (Figure 4).

When we compared the ADE and NDE forests using the quantitative matrix (richness and abundance), we observed differences in floristic composition in both southern and eastern Amazonia (PerMANOVA, NDE versus ADE in general, $F_{(1,17)} = 2.99$, $r^2 = .16$, $p < .001$; NDE-S versus ADE-S, $F_{(1,5)} = 2.03$, $r^2 = .34$, $p < .001$, and NDE-E versus ADE-E, $F_{(1,11)} = 5.29$, $r^2 = .35$, $p = .002$).

Partitioning the abundance matrix by diameter class indicated that there were significant differences between ADE and NDE (all sites combined) for the larger diameter classes (> 40 cm). The smallest diameter classes of ADE and NDE forests, in both southern and

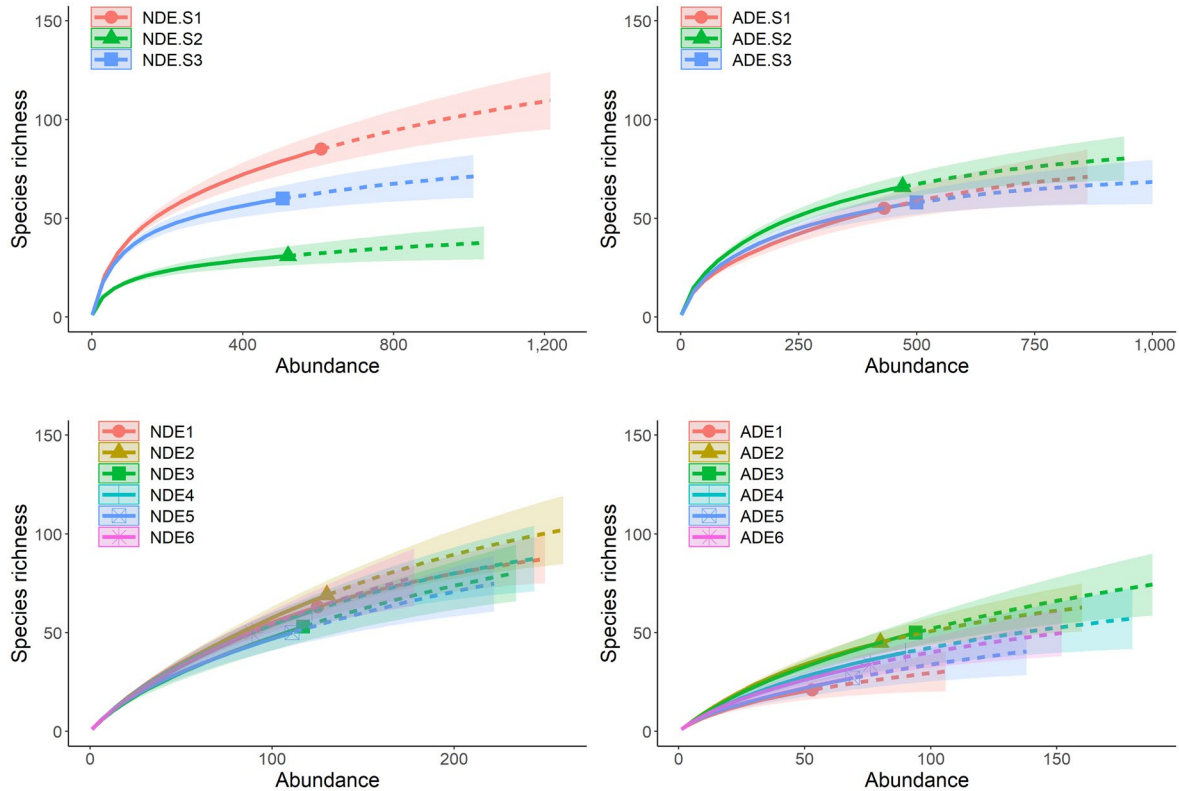


FIGURE 3 Rarefaction curves for Amazonian Dark Earth (ADE) and non-Dark Earth (NDE) forests located in eastern (NDE.E and ADE.E) and southern Amazonia (NDE.S and ADE.S). Continuous and dashed lines refer to observed and extrapolated sample coverage, respectively, and the area around the curve represents a 95% confidence interval

TABLE 1 Total observed and estimated richness (Jackknife1); Shannon diversity index (H'); Hurlbert evenness (PIE = probability of interspecific encounter); abundance, richness/ha (richness per hectare); biomass (average aboveground biomass Mg ha^{-1}); and families (number of families sampled in Amazonian Dark Earth (ADE) and non-Dark Earth (NDE) forests in southern (S) and eastern (E) Amazonia, Brazil. *SD* = standard deviation

Sites	Total estimated richness	Total richness	H'	PIE	Abundance	Richness/ha (SD)	Biomass (SD)	Families
NDE-S	158	122 ^a	3.69 ^a	.95 ^a	1,634	59 (27)	152 (7)	42
NDE-E	256	171 ^b	4.42 ^b	.98 ^b	694	146	308 (48)	40
ADE-S	171	117 ^a	3.60 ^a	.95 ^a	1,401	60 (5)	214 (66)	40
ADE-E	199	132 ^b	4.22 ^b	.97 ^b	462	118	135 (78)	39

Note.: Numbers followed by different letters in the same column differ significantly at $p < .05$ by the permutational multivariate analysis of variance (PerMANOVA) test.

eastern Amazonia, were more similar to one another (Table 2). At the forest level, in general, we observed low similarity between the first (smallest) and the third (largest) diameter classes (Supporting Information Tables S6 and S7). However, there was no significant difference based on the Bonferroni p -value.

Four distinct groups were formed in the NMDS analysis (see sampling coverage in Supporting Information Figure S1): the forests of eastern Amazonia were clearly separated from the forests of southern Amazonia on axis 1 ($r^2 = .35$) and ADE and NDE forests of each region individually were grouped on axis 2 ($r^2 = .48$) (Figure 5 and Supporting Information Figure S1), with the two axes representing 83.3% of the proportion of the variance in the original distance matrix.

We found a high number of useful and edible species in ADE and NDE forests in both regions. The proportion of edible species tended to be higher in the ADE forests of eastern and southern Amazonia (Table 3). In eastern Amazonia, we found 31% edible species in NDE forests and 33% in ADE forests. In southern Amazonia, we observed 25% edible species in NDE forests and 31% in ADE forests (Table 3 and Supporting Information Tables S8 and S9). Among them, the useful species *Hymenaea courbaril* (West Indian locust = fruit/food) and *Spondias mombin* (locally known as *Taperebá* = fruit/food) occurred more broadly, dominating the floristic composition of ADE forests of both regions. At a local scale, we observed useful species such as *Bertholletia excelsa* (Brazil nut, food), *Inga alba* and *Inga edulis* (fruit/food) shared among the sampling units of Amazonia and *Buchenavia*

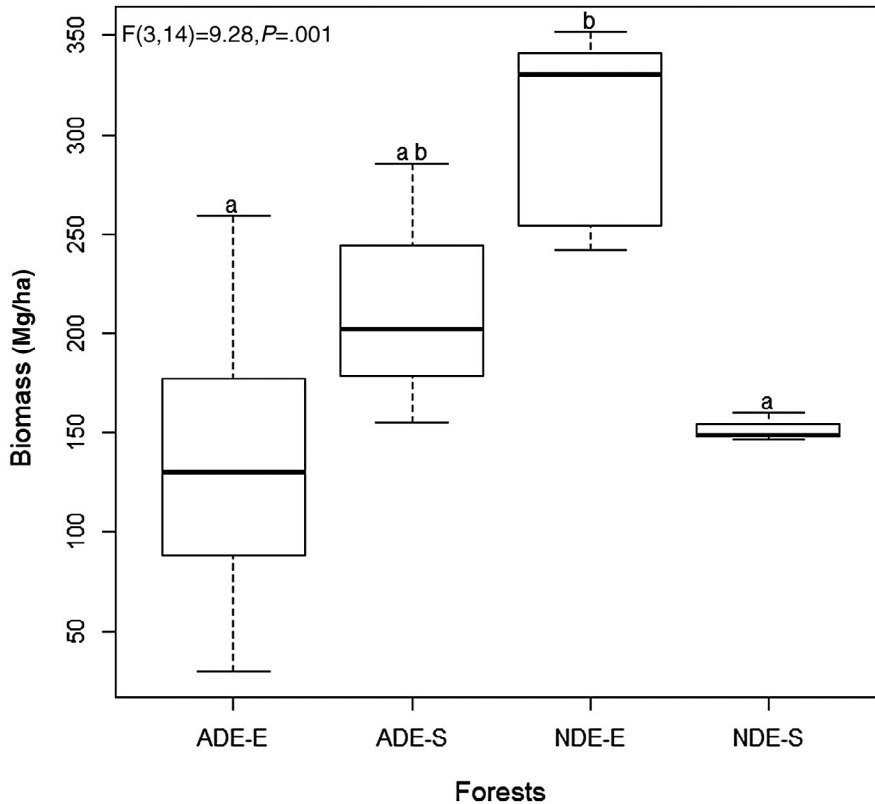


FIGURE 4 Biomass comparison (Mg ha^{-1}) between Amazonian Dark Earth (ADE) and non-Dark Earth (NDE) forests in eastern (ADE-E and NDE-E) and southern Amazonia (ADE-S and NDE-S), Brazil. Different letters indicate differences significantly at $p < .05$

TABLE 2 Permutational multivariate analysis of variance (PerMANOVA) comparing the floristic matrix between diameter classes in Amazonian Dark Earth (ADE) and non-Dark Earth (NDE) forests in southern (ADE-S and NDE-S) and eastern Amazonia (ADE-E and NDE-E), Brazil, including the F -statistic, R^2 and p -value

Sites	Classes (cm)	F	R^2	p
ADE versus NDE (all sites)	10–20	1.28	.14	.19
	> 20–40	1.75	.18	.03
	> 40	2.00	.20	< .001
ADE-S versus NDE-S	10–20	1.62	.29	.17
	> 20–40	2.20	.35	.10
	> 40	.57	.12	.80
ADE-E versus NDE-E	10–20	2.55	.56	.33
	> 20–40	2.62	.57	.04
	> 40	2.78	.58	.04

Note.: Value in bold indicates statistically significant difference according to Bonferroni test. [p -values divided by three ($.05/3 = .0167$)].

tomentosa Eichler, *Myrciaria floribunda* (H.West ex Willd.) O.Berg and *Psidium sartorianum* (O.Berg) Nied. shared among the sampling units of southern Amazonia.

4 | DISCUSSION

This is the first landscape-scale comparison of soil and vegetation from ADEs and NDEs of eastern and southern Amazonia and one

of the few studies to focus on mature forests growing on ADEs. Previous studies focused on secondary forests or agroforestry on ADE and NDEs within a region (Junqueira et al., 2010). The floristic composition and aboveground biomass of ADEs of our study show strong differences from the surrounding NDE soils. The dissimilarities in floristic composition between ADEs and NDEs increase the regional species richness, an important consideration for regional biodiversity conservation. These findings highlight the small-scale long-term legacy of pre-Columbian inhabitants on the soils and vegetation of Amazonia.

Species richness in ADE and NDE forests was within the range recorded in forests in both southern (Kunz, Ivanauskas, Martins, & Silva, 2008; Kunz, Martins, & Ivanauskas, 2010; Lopez-Gonzalez, Lewis, Burkitt, & Phillips, 2009) and eastern Amazonia (Gonçalves & Santos, 2008). However, in general, the southern Amazonian forests showed species richness approximately two or three times lower than those of central Amazonia (Korning, Thomsen, & Ollgard, 1991; S. G. W. Laurance et al., 2010; Valencia, Balslev, & Paz Y Miño C, 1994). The southern Amazonian vegetation growing on dystrophic soils has been considered hyperdynamic (region with high dynamism from major intra- and inter-year climate variation), with lower species richness (Marimon et al., 2014); in contrast, forests located on higher fertility soils of Andean-Amazon lowland forests are dynamic but have higher species richness. Low species richness may result from more complex trophic interactions in environments with resource limitations, such as water and nutrients (Huston, 1980).

Our study sites in both southern and eastern Amazonia showed neither a positive nor negative soil fertility effect on the richness

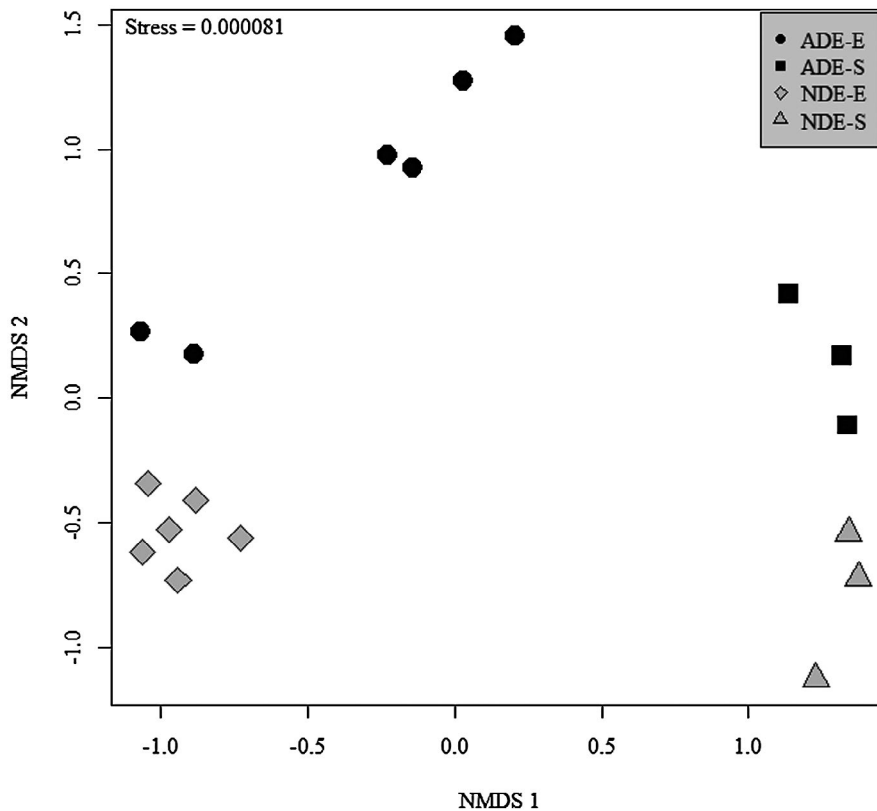


FIGURE 5 Bi-dimensional ordination (NMDS = non-metric multidimensional scaling) of Amazonian Dark Earth (ADE) and non-Dark Earth (NDE) forests based on the species-abundance matrix for southern (ADE-S and NDE-S) and eastern Amazonia (ADE-E and NDE-E), Brazil. Stress = .000081

TABLE 3 Edible and useful species sampled in forests growing on Amazonian Dark Earth (ADE) and non-Dark Earth (NDE; control) in eastern Amazonia (ADE-E and NDE-E, state of Pará) and southern Amazonia (ADE-S and NDE-S, state of Mato Grosso), Brazil. For more details see Supporting Information Tables S8 and S9

Sites	Species total	Edible species	% Edible species	Useful species	% Useful species
NDE-E	171	53	31	99	58
ADE-E	132	43	33	75	57
NDE-S	122	30	25	71	58
ADE-S	117	36	31	71	60

of woody species, suggesting that long-term fertilization does not contribute to increasing local richness in plots within ADE patches. However, the dissimilarities in floristic composition between ADEs and NDEs in the present study indicate a contribution to the regional species richness. In Amazonia, in the case of a positive effect, ADE forests with fertile soil and higher productivity (Aragão et al., 2009; Cunha et al., 2007) would be similar to the forests of western Amazonia (close to the Andes), where Gentry (1988) sampled species richness between 165 and 300 per hectare on the more fertile soils of the region. In the case of a negative effect, the fertilization could be favouring the growth of species that better compete on mesotrophic soils, and therefore, decreasing species richness, as predicted in the enrichment paradox (Rosenzweig, 1971), as observed in experiments with artificial fertilization (Tilman & Isbell, 2015), and in field

observations in tropical forests (Huston, 1980; Nadeau & Sullivan, 2015). In our case, the assembly of local species may be allowing a balanced exchange of tree species between the ecosystems of ADE and NDE forests, which would explain the similar local species richness between forest types.

Among the families assessed in our study, Fabaceae showed the largest number of species in all forests as also observed by Junqueira et al. (2010). This family is usually among the most important in terms of species number of the Amazonian flora (Valencia et al., 1994). According to ter Steege et al. (2006), sites with poor soils in South America have fewer species of Fabaceae; however, seed mass in these species was 20% higher, which could be a possible explanation for the high importance and success of Fabaceae in South American ecosystems with dystrophic soils. Nevertheless, both ADE forests on mesotrophic soil and NDE forests on dystrophic soil showed Fabaceae as the family with the largest number of species. A possible explanation for the higher number of species in Fabaceae and Annonaceae families in our study could be related to their adaptability and early appearance in South America (Doyle & Le Thomas, 1997; Doyle & Luckow, 2003; Lavin & Luckow, 1993). Alternatively, the occurrence of the species *Apuleia leiocarpa*, *Spondias mombin* and *Maclura tinctoria* only in ADE forests could be related to the preference of these species for more fertile soils, management of these species by indigenous communities in the past (Clement, 1999), or both. However, only *S. mombin* was cited as semi-domesticated in the study by Junqueira et al. (2010) with secondary forests on ADE soil. *S. mombin* was observed among the main tree species with seeds or fruits that are commonly eaten or used by humans

in anthropogenic soils in Bolivia (Paz-Rivera, 2009); nevertheless, it was not exclusive to ADE, suggesting that the inhabitants could have enriched the NDE with edible species.

Regarding the difference in the composition matrix, the mesotrophic soil (medium fertility) is possibly acting as a species filter that determines the difference in species composition between ADE and NDE forests. Hence, in ADE environments with higher nutrient availability and where pyrogenic carbon may increase soil water holding capacity (Lehmann & Joseph, 2009), tree species, such as *Hymenaea courbaril*, *Copaifera langsdorffii* and *Apuleia leiocarpa*, may have greater competitive advantages. Thus, the mesotrophic soils of the ADEs may be a key factor that affects species composition in the present study, selecting the species most favourable for the trophic conditions of these ecosystems.

There was a significant difference between tree size in ADE and NDE forest plots. In the smallest diameter classes, there was greater sharing of species in the tree community among species typical of ADE and those typical of NDE. This pattern could indicate that a fertility filter acts by favouring size, by selecting the larger species when they begin to surpass the smallest diameter classes and subsequently dominate the community. Alternatively, the similarity between the smallest size classes for ADE and NDE may indicate ADE composition will eventually become more NDE-like as the small classes mature.

The aboveground biomass of ADE forests sampled in eastern Amazonia was similar to those observed in open, alluvial and dense forests in southwestern and central Amazonia (Cummings, Boone Kauffman, Perry, & Flint Hughes, 2002; W. F. Laurance et al., 1999). However, as we observed, there is high variation in biomass values in different regions in Amazonia, in part due to differences in tree height (Feldpausch et al., 2012). Two of the ADE-S (southern) forests sampled also showed relatively high biomass values, similar to those of microregions in southwestern and eastern Amazonia and the higher biomass NDE-E (eastern) sites in the present study. The considerable number of species and individuals of the family Fabaceae (*Hymenaea courbaril*, *Copaifera langsdorffii* and *Apuleia leiocarpa*), which usually have high wood density, also contribute to the high biomass of these forests (ter Steege et al., 2006). These results show the importance of soil fertility in the structural development of forests and support studies that considered soil fertility as one of the biomass predictors in Amazonia (Doughty et al., 2013; S. G. W. Laurance et al., 2010; Vicca et al., 2012). Moreover, the high variation in biomass stocks in ADE forests in southern and eastern Amazonia could also be related to each 'cultural forest' having a unique history of creation, use, and selection of plants and post-Columbian regrowth (Balée, 2013). Due to the long history of post-colonial land-use in the Santarem region, past land-use prior to formation of the FLONA reserve, with colonizers often selecting ADEs for production, could have reduced the biomass at the ADE-E sites.

We observed few useful species shared among different ADE forests at the Amazon Basin scale [only *Acrocomia aculeata* (Jacq.) Lodd. ex Mart., *Guazuma ulmifolia* Lam. *Inga laurina*, *Cupania scrobiculata* Rich., *Pseudolmedia macrophylla* Trécul, *Spondias mombin* and *Hymenaea courbaril* as edible], usually explained by the low similarity

between the two regions. We observed a moderate number of useful species at a local scale. The slightly higher number of useful species in the ADE (proportionally) in eastern Amazonian plots may be due to the differences in how ADE and NDE sites were historically managed by pre-Columbian people or by the distance between the studied areas (Maezumi et al., 2018). The relatively small ADE areas were often used for annual crops, while the surrounding area may have been enriched in useful tree species (Paz-Rivera, 2009). There is evidence of enrichment of edible plants in ADE soils (Maezumi et al., 2018). Some factors that could explain the low similarity between useful species at the Amazon Basin scale include (a) low species adaptability to a new climate; (b) limited forms of seed transport between the two regions; (c) or if the ADE forests of the Mato Grosso region were colonized by indigenous populations with ethnicity or from regions different from those of eastern Amazonia. Souza et al. (2019) argued that differences in landuse and socio-political organization may be key to understanding vulnerability versus resilience to environmental stress; by comparing archaeological data with data from palaeoclimate proxies and regional-scale burning, they showed that some Amazonian cultures flourished during periods of climate change, whereas others collapsed. Defining 'useful' and accounting for regional variation in use are challenges since a large number of useful species are used by different indigenous populations in other regions of Amazonia (Boom, 1985; Prance et al., 1987), with up to 82% of the species with different utility levels occurring in only 1 ha. In the present study, this value varied between 57 and 60%.

Studies combining archaeology, ecology and botany identified variation in early practices that may have resulted in regional variation in the creation, use and subsequent post-abandonment regrowth of ADEs. An interdisciplinary study demonstrated that pre-Columbians enriched the forests c. 2,500 years ago with above 30% increase in edible plants that persist to present (Maezumi et al., 2018). However, we do not yet know which species have distributions influenced by humans (Gordon, Barrance, & Schreckenber, 2003). A well-known example is the strong relationship between the distribution of the Brazil nut (*Bertholletia excelsa*) and the range of human populations in the Amazon Basin (Levis et al., 2017; Mori & Prance, 1990; Shepard & Ramirez, 2011). Therefore, the distribution of other species with potential fibre, medicinal and food use, such as *S. mombin* (currently used in sweets and juices), *H. courbaril* (cakes and bread), *Aspidosperma desmathum* (medicinal), *Psidium sartorianum* (fruit) and *Cochlospermum orinocense* (fibres), may have been altered by past indigenous people. In addition, the large numbers of *P. sartorianum*, *Cheilochlinium cognatum* and *Myrciaria floribunda* in ADE forests in southern Amazonia suggest high adaptability to this soil type or management by pre-Columbian people.

5 | IMPLICATIONS FOR CONSERVATION

ADE soils throughout Amazonia, including those in our study, are under risk of loss, as they are located at the Brazilian agricultural frontier, where there is accentuated deforestation and fire at the Amazon/

Cerrado savanna zone of transition (ZOT; Alencar et al., 2004; Nogueira, Fearnside, Nelson, & Franca, 2007; Nogueira, Nelson, Fearnside, França, & Oliveira, 2008). In eastern Amazonia, where the flora differs from the ZOT, this soil type with high fertility and potential rapid biomass accumulation has been used by contemporary farmers for subsistence agriculture, rubber tree plantation (Schroth, Coutinho, Moraes, & Albernaz, 2003; Weinstein, 1983), and timber (Junqueira et al., 2010, 2011). To address these threats, conservation programmes should include these unique environments to improve understanding of local pre-Columbian histories, identity, and role in regional floristic diversity. Moreover, ADE forests have peculiar characteristics such as: (a) high productivity and biomass (preserved sites), usually within a matrix of dystrophic soils (Cunha et al., 2007; Doughty et al., 2013; Falcão & Borges, 2006; Glaser & Birk, 2012; Madari et al., 2009; M. G. G. Silva, 2011); (b) presence within a region of climatic uncertainties (Bonan, Levis, Sitch, Vertenstein, & Oleson, 2003; Feldpausch et al., 2016; Gloor et al., 2015); (c) potential as a long-term carbon sink (Lehmann et al., 2008); and (d) importance for future studies to reduce the use of chemical fertilizers in agriculture (Hunt, Dupont, Sato, & Kawabata, 2010).

6 | CONCLUSION

In ADE forests, the absence of long-term soil fertilization effects on local diversity (species number) points to the importance of the regional species pool in determining the diversity at plot scales. However, the dissimilarities in floristic composition between ADEs and NDEs indicate a contribution at regional scales to species richness. Moreover, the marked difference in species composition and structure (biomass) between ADE and NDE forests shows that soil fertility can influence other community attributes in Amazonian forests. Therefore, it is important to consider the role of changes in nutrient levels at different scales and ecosystems (e.g., forest burning). In addition, the differences in composition and abundance linked to tree diameter classes suggest a legacy influence of historical land-use and soil enrichment in ADE on the structure of ADE forests (highest biomass), which may have favoured some species, for example, *Hymenaea courbaril*, *Copaifera langsdorffii* and *Apuleia leiocarpa*. The presence of a relatively large number of useful and edible species at a local scale, associated with both ADE and NDE forests, suggests indigenous populations likely used ADE for crop cultivation and the adjacent NDE forests for agroforestry. Combined, our results indicate a pre-Columbian, small-scale, long-term, land-use legacy in Amazonian forests.

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ORCID

Edmar Almeida de Oliveira  <https://orcid.org/0000-0002-6446-3376>

Ben Hur Marimon-Junior  <https://orcid.org/0000-0002-6359-6281>

Beatriz Schwantes Marimon  <https://orcid.org/0000-0002-3608-3739>

José Iriarte  <https://orcid.org/0000-0002-8155-5360>

Paulo S. Morandi  <https://orcid.org/0000-0001-8151-7738>

S. Yoshi Maezumi  <https://orcid.org/0000-0002-4333-1972>

Denis S. Nogueira  <https://orcid.org/0000-0001-8893-7903>

Luiz E. O. C. Aragão  <https://orcid.org/0000-0002-4134-6708>

Izaías Brasil da Silva  <https://orcid.org/0000-0002-6975-3460>

Ted R. Feldpausch  <https://orcid.org/0000-0002-6631-7962>

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BIOSKETCH

Edmar Almeida de Oliveira is a Biologist, with a MSc in Ecology and Conservation by the University of Mato Grosso States (UNEMAT), and PhD in Biodiversity and Biotechnology from the post-graduation program Bionorte network. He was a postdoctoral researcher and field project coordinator for the research project Global Ecosystems Monitoring (GEM) in Nova Xavantina, Brazil. He has experience in botany and plant ecology in gallery forest, flooded forests, semideciduous

forest, seasonal evergreen and Amazonian forests (upland forest and Amazonian Dark Earth), cerrado sensu strictu (Brazilian savanna) and cerrado (savanna woodland). He also has experience with carbon and community dynamics, ecosystem and community ecology, and Amazonian plant biodiversity. Recently, he was the technical coordinator of flora monitoring at the Belo Monte Plant. Currently, he is developing a postdoctoral position in the PELD project in Amazon-Cerrado transition zone.

Ben Hur Marimon-Junior is a professor at the State University of Mato Grosso, Brazil. His expertise is in forest ecology, with a focus on biogeochemical cycles, carbon stocks, pyrogenic carbon for plant nutrition, biodiversity and ecosystem function. He is rated a PQ1 productivity fellow from the National Council for Scientific and Technological Development of Brazil (CNPq). He has over 25 years of research and publication experience. His research findings have been published in the most important scientific journals, including *Science* and *Nature*.

Beatriz Schwantes Marimon is a professor at the State University of Mato Grosso, Brazil. Her work focuses on forest ecology and management in the Amazonia-Cerrado transition zone to understand the effect of climate change on plant communities. The results of more than 25 years of her researches have been published in high-impact scientific journals, including *Science* and *Nature*. She is currently rated a PQ1 productivity fellow at the National Council for Scientific and Technological Development of Brazil (CNPq).

José Iriarte is Professor of Archaeology at the University of Exeter. He is an archaeologist and archaeobotanist with a strong track record of research on human-environmental interactions, the development of agricultural economies, and the emergence of complex societies in lowland South and Central America. Iriarte has extensive experience in directing and participating in a wide range of international multidisciplinary projects integrating archaeology, archaeobotany, palaeoecology, palaeoclimate, soil science, remote sensing (Lidar), ancient DNA, and modern ecology across Latin America. Recently, the work of his research group on lowland South American landscapes has documented the third global event of rice domestication in Amazonia (Nature Ecology and Evolution 2018), chartered unexplored regions of Amazonia documenting earth-building societies along its entire southern rim predicting to have reached 5 million people in pre-Columbian times (Nature Communications 2018), revealed the lasting repercussions of polyculture agroforestry on Amazonian Dark Earths (PNAS 2014, Nature Plants 2018), assessed the role of climate in cultural developments across Amazonia (Nature Ecology and Evolution 2019) as well as the human footprint on the expansion of Araucaria forests in southern Brazil (Scientific Reports 2018). Iriarte directs the University of Exeter Tropical Archaeobotany and Paleoeology Laboratory.

Paulo S. Morandi is a Biologist with a MSc in Ecology and Conservation and PhD in Biodiversity and Biotechnology, with a joint PhD at the University of Leeds, UK. After his PhD, he completed two years of postdoctoral research in Ecology at the Universidade do Estado de Mato Grosso – BR (UNEMAT). His studies have aimed at understanding the diversity, biomass and species composition of savanna and forest vegetation in the Cerrado-Amazon transition, as well as in the Cerrado biome, and the ecological relationship with environmental predictors. He is currently a Special Visiting Professor at the UNEMAT, where he teaches classes on Plant Morphology and Systematics, Ecology and the use of Statistical Methods.

S. Yoshi Maezumi is a Paleoecologist and Archaeologist with a Masters in Analytical Archaeology and a Doctorate in Physical Geography. After completing her PhD, she held a 3-year post-doctoral fellowship in the Department of Archaeology at the University of Exeter. The results of her post-doctoral research were published in *Nature Plants*, *Science*, *Nature Ecology and Evolution*, and *Scientific Reports*. Following her post-doctoral research she held 1-year Lectureship in Geography and Geology the University of the West Indies, Jamaica. She is currently a Marie Curie Research Fellow for her project FIRE: Fire Intensity in Rainforest Ecotones at the Institute for Biodiversity and Ecosystem Dynamics at the University of Amsterdam.

Denis Silva Nogueira has a BSc in Biological Sciences (degree) (2008), MSc in Ecology and Conservation (2011) by the State University of Mato Grosso, and PhD in Ecology and Evolution from the Federal University of Goiás (2015). He has experience in the ecology of aquatic ecosystems, aquatic insects, community ecology, biomonitoring and environmental assessment, methods of estimating diversity, numerical ecology and biostatistics. He was a postdoctoral researcher at CNPq, where he studied the dynamics of forests in the Amazon-Cerrado transition in Mato Grosso, in partnership with researchers from the State University of Mato Grosso, Nova Xavantina Campus and the University of Leeds (2015-2017). He is currently a biology professor, D-I, level 1, at the Federal Institute of Mato Grosso, Campus of Primavera do Leste, Mato Grosso, Brazil.

Luiz E. O. C. Aragão has a PhD in Remote Sensing from the National Institute for Space Research (2004). He is Senior Scientist at the National Institute for Space Research (INPE), where he serves as head of the Remote Sensing Division and coordinates the TREES Research Group (Tropical Ecosystems and Environmental Sciences group). Aragão is the President of the Scientific Committee of the LBA Program and Coordinator

of the Brazilian Symposium on Remote Sensing. He published as the first author in the journals *Science* and *Nature*. He has experience in the area of Tropical Ecosystems and environmental sciences, with an emphasis on Remote Sensing, focused on the following themes: carbon dynamics, climate and environmental changes, ecosystem ecology and landscape, remote sensing of forest disturbances.

Izaías Brasil da Silva has a BSc in Biology and MSc in Ecology from the Federal University of Acre, Brazil. He has experience in Systematic Botany, Forest Inventory, Archaeology, and he works with rural communities in the Amazon rainforest. Izaías currently works with Forest Inventory and is planning community development in Acre, Brazil. Izaías has been appointed to work as a MAP-Fire Research Assistant for coordinating the field inventories and data analysis.

Ted R. Feldpausch has a PhD in Forest Ecology / Soil Science from Cornell University and is an Associate Professor at the University of Exeter, UK, and an affiliated professor at the National Institute of Amazonian Research, Brazil and the State University of Mato Grosso, Brazil. He has expertise in the ecology of tropical forests and savannas and coordinating large interdisciplinary research projects integrating ecosystem science, biogeography, soil science, palaeoecology, archaeobotany, modelling, and remote sensing. His research spanning 20 years on themes including biogeochemical cycles, large-scale drought effects, fire and pyrogenic carbon has been published in high-impact journals including *Science* and *Nature*. His work across the tropics has contributed to the development of large international forest plot networks, including the Amazon Forest Inventory Network (RAINFOR) and the African Tropical Rainforest Observation Network (AfriTRON) and the data curation and management platform ForestPlots.net. His ongoing projects explore the effect of modern and centennial-scale fire on tropical forests, forest disturbance and regeneration, and the effect of lightning on tropical forest tree mortality and forest function.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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