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 Maezumi²,³ | Denis S. Nogueira⁴ | Luiz E. O. C. Aragão⁵,⁶ | Izaias Brasil da Silva⁷ | Ted R. Feldpausch¹,⁵

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.
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; Levis et al., 2017; McMichael et al., 2012). 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 (Neve, 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; Neve 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 phytosociometric type represents most vegetation of northern Brazil and is characterized by a closed canopy, large individual trees, and high temperature and humidity (Veloso, 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 (Stenberg, 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 Tapajos National Forest (FLONA Tapajos), 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...

---
et al., 2003). ADEs are estimated to cover c. 1–3% (6,000–18,000 km$^2$) 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 km$^2$). 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 \([\text{pH(H}_2\text{O)}, \text{P, K, Ca, Mg and Al}], \text{sum of bases (SB, cmolc/dm}^3\text{), cation exchange capacity (CEC, cmolc/dm}^3\text{)}\) and the ratios \(\text{Ca:Mg, Al}^3_\text{+ H:CEC (%), Ca:CEC (%) and Mg:CEC (%) (Supporting Information Table S2)}\) 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 \(D \geq 10 \text{ cm at breast height (1.3 m)}\) 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) $B = 0.509 \times (\rho D^2 H)$; where $D$ is individual diameter (cm) at 130 cm height or above deformities and buttress roots, $H$ is total tree height (m), and $\rho$ 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 $\left[ H = a(1 - \exp(-b D^2)) \right]$ 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, Bahia, Boêm, & 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$_2$O), P, K, Ca, Mg and Al], sum of bases, organic matter, cation exchange capacity, and the ratios Ca:Mg, Al$^3+$/H: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 scalin 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 Al$^3+$ + 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 Areccaceae 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.) Wild. 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, Steyerm. & 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, $F_{(1, 9)} = 2.03, r^2 = .34, p < .001$, 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
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*
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
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 southwestern 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 Tréc., 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 palaeoclimatic 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, & Schreckenberg, 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, Chelochlinium 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, Duponte, 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*, *Copaefera langsdorffii* and *Apuleia leio-carpa*. 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.

ACKNOWLEDGMENTS

We thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for financial support through the Science Without Borders Program to TRF (PVE 177/2012) and field support from the Natural Environment Research Council (NERCNE/N011570/1). We thank the University of Exeter, UK, for receiving EAO during the writing of the present manuscript and the BIOCEV Serviço de Meio Ambiente for the support during the corrections. The Brazilian Council for Scientific and Technological Development (CNPq) granted LEOCA (305054/2016-3), BHM-Junior and BSM research productivity fellowships (PQ1) and funded the projects Programa de Pesquisas Ecológicas de Longa Duração (PELD) (CNPq 403725/2012/7 and 441244/2016-5) and Research Program in Biodiversity (PPBio) (457602/2012-0). We thank RAINFOR/Forestplot.net for the scientific support, and ReFlorRede Floresta (FAPEMAT #0589267/2016) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 for the financial support. The Laboratory of Plant Ecology of Nova Xavantina-MT (LABEV) provided logistic support, including undergraduate and graduate students assisting with fieldwork and data processing. Funding for research at the FLONA Tapajós was supported by a European Research Council Consolidator Grant to Ji (ERC_Cog 616179). Research at the FLONA-Tapajós was conducted under permit 01506.004836/2014-69 from the Instituto do Patrimônio Histórico e Artístico Nacional (IPHAN) and Chico Mendes Institute for Biodiversity Conservation (ICMBio) permit 106/14-FNT. J. G. de Souza produced the map.

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
Izaias Brasil da Silva https://orcid.org/0000-0002-6975-3460
Ted R. Feldpausch https://orcid.org/0000-0002-6631-7962

REFERENCES

Alencar, A., Nepstad, D., Mcgrath, D., Moutinho, P., Pacheco, P., Dias, M. D. C. V., & Filho-Soares, B. (2004). Desmatamento na Amazônia: Indo além da “emergência crônica”. Belém, PA: IPAM, PA, Brazil.
Alves, D. T. (2018). Dark Earth plant management in the Lower Tapajós (PhD thesis). University of Exeter.
Anderson, M. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology, 26*, 32–46.
Aragão, L. E. O. C., Mahi, Y., Metcalfe, D. B., Silva-ESpejo, J. E., Jiménez, E., Navarrete, D., ..., Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences, 6*, 2441–2488. https://doi.org/10.5194/bg-6-2441-2009
Arroyo-Kalin, M. (2010). The Amazonian formation: Crop domestication and anthropogenic soils. *Diversity, 2*, 473–504. https://doi.org/10.3390/d2040473
Balée, W. (2013). Cultural forests of the Amazon: The historical ecology of people and their landscapes. Tuscaloosa, AL: The University of Alabama Press.
Barlow, J., Gardner, T. A., Lees, A. C., Parry, L., & Peres, C. A. (2012). How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for
Edmar Almeida de Oliveira is a Biologist, with a MSc in Ecology and Conservation by the University of Mato Grosso (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 cerradão (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.

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, 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 Communications 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 2018) and 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 Paleoecology 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.

**How to cite this article:** de Oliveira EA, Marimon-Junior BH, Marimon BS, et al. Legacy of Amazonian Dark Earth soils on forest structure and species composition. Global Ecol Biogeogr. 2020;00:1–16. [https://doi.org/10.1111/geb.13116](https://doi.org/10.1111/geb.13116)