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Michael W. Palace
University of New Hampshire, Durham, michael.palace@unh.edu

C. N. H. McMichael
University of Amsterdam

Bobby H. Braswell
University of New Hampshire, Durham, rob.braswell@unh.edu

S. C. Hagen
Applied GeoSolutions

M. B. Bush
Florida Institute of Technology

Comments

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Authors

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Ancient Amazonian populations left lasting impacts on forest structure

M. W. Palace,[1,2,]† C. N. H. McMichael,[3] B. H. Braswell,[1,4] S. C. Hagen,[4] M. B. Bush,[5]
E. Neves,[6] E. Tamanaha,[7] C. Herrick,[1] and S. Frolking[1]

[1]*Earth Systems Research Center, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, New Hampshire 03834 USA*
[2]*Department of Earth Science, College of Engineering and Physical Sciences, University of New Hampshire, Durham, New Hampshire 03834 USA*
[3]*Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 904 Science Park, 1098XH Amsterdam, The Netherlands*
[4]*Applied GeoSolutions, 55 Main Street, Suite 125, Newmarket, New Hampshire 03857 USA*
[5]*Department of Biological Sciences, Florida Institute of Technology, 150 W. University Boulevard, Melbourne, Florida 32901 USA*
[6]*Museu de Arqueologia e Etnologia, Universidade de São Paulo, Av. Prof. Almeida Prado, 1466, Sao Paulo, Sao Paulo 05508-070 Brazil*
[7]*Laboratório de Arqueologia, Instituto de Desenvolvimento Sustentável Mamirauá, Estrada do Bexiga, 2.584, Bairro Fonte Boa, Tefé, Amazonas 69553-225 Brazil*

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Abstract. Amazonia contains a vast expanse of contiguous tropical forest and is influential in global carbon and hydrological cycles. Whether ancient Amazonia was highly disturbed or modestly impacted, and how ancient disturbances have shaped current forest ecosystem processes, is still under debate. Amazonian Dark Earths (ADEs), which are anthropic soil types with enriched nutrient levels, are one of the primary lines of evidence for ancient human presence and landscape modifications in settings that mostly lack stone structures and which are today covered by vegetation. We assessed the potential of using moderate spatial resolution optical satellite imagery to predict ADEs across the Amazon Basin. Maximum entropy modeling was used to develop a predictive model using locations of ADEs across the basin and satellite-derived remotely sensed indices. Amazonian Dark Earth sites were predicted to be primarily along the main rivers and in eastern Amazonia. Amazonian Dark Earth sites, when compared with randomly selected forested sites located within 50 km of ADE sites, were less green canopies (lower normalized difference vegetation index) and had lower canopy water content. This difference was accentuated in two drought years, 2005 and 2010. This is contrary to our expectation that ADE sites would have nutrient-rich soils that support trees with greener canopies and forests on ADE soils being more resilient to drought. Biomass and tree height were lower on ADE sites in comparison with randomly selected adjacent sites. Our results suggested that ADE-related ancient human impact on the forest is measurable across the entirety of the 6 million km^2 of Amazon Basin using remotely sensed data.

Key words: Amazonia; Amazonian Dark Earths; ancient people; anthrosols; drought; forest structure; maximum entropy modeling; MODIS; pre-Columbian impact; terra preta; tropical forests.

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† **E-mail:** michael.palace@unh.edu

INTRODUCTION

The Amazon Basin contains the largest continuous rainforest in the world (~6 million km^2) and now constitutes 40% of this ecotype globally (Olson et al. 2001, Keller et al. 2004). The long-term resilience of these forests to climate change is uncertain (Betts et al. 2004, Malhi et al. 2009), but it is certain that humans have the capacity through deforestation to radically alter Amazonia's biodiversity and carbon storage capacity (Nobre et al. 1991, Goulding et al. 1996, Werth and Avissar 2002, Palace et al. 2012, Bustamante et al. 2016, Poorter et al. 2016). Forest structural heterogeneity in the physical form of the canopy geometry, tree heights, and species composition (Salati and Vose 1984, Terborgh 1992, Brown et al. 1995, Chave et al. 2001, Houghton et al. 2001, Rice et al. 2004) is matched by both an often-overlooked variability in habitats and a divergent history of pre-historic use. A key question for ecologists is to what extent do the differences in modern forests reflect natural long-term vegetation dynamics, edaphic processes, or human activity?

Estimates of the pre-Columbian indigenous population of the Amazon Basin lowlands are highly uncertain, widely varying, and have been the subject to considerable controversy (Brondizio 2003, Meggers 2003, Bush and Silman 2007, Clement et al. 2015). Estimates of pre-Columbian populations for the Amazon Basin have ranged from 500,000 to 10 million (Comas 1951, Moran 1974). Multiple mid-range estimates from 6.8 to 8 million people have been proposed (Denevan 1970, 1992, Clement et al. 2015). One school of thought suggested that Amazonia was a counterfeit paradise whose lush vegetation hid nutrient-poor soils incapable of supporting large populations and complex societies (Meggers 1971, 2003). In contrast, others have found indications of large populations with hierarchical social organization and intensive agricultural practices (Roosevelt 1991, Heckenberger et al. 2003*a*, Heckenberger 2004, Balée and Erickson 2006) Though the debate between these two groups was hotly contested, new evidence indicates a spatially heterogenic settlement patterns across Amazonia (Meggers 2003, Heckenberger et al. 2003*b*, McMichael et al. 2012*a*, Clement et al. 2015). One point of agreement among the proponents of the extreme points of view, as well as those in between, is the scarcity of data regarding the pre-European societies of Amazonia (Denevan 2014).

The European invasion brought depopulation, exploitation, and slavery to Amazonia. Diseases such as smallpox, influenza, and measles decimated indigenous populations, by as much as 90% in some parts of Latin America (Henige 1998, Denevan 2001). Abandonment of the most accessible sites was widespread, partly as a direct consequence of population collapse and partly to avoid further interaction with Europeans (Dobyns 1966, Crosby 2004, Chambouleyron et al. 2011). The net effect of site abandonment was that lands that had been cleared and cultivated became successional forest (Chambouleyron et al. 2011). By the eighteenth century, when the first naturalists traveled to the area, they found formerly occupied places covered by forest and Amerindian societies scattered along the headwaters of the tributaries of the Amazon. Plant management, including cultivation of domesticated plants, is known to have been practiced in lowland Amazonia for thousands of years before European arrival (Bush et al. 1989, Brugger et al. 2016, Bush and McMichael 2016).

Along the Amazon River, the flooded forest (*várzea*) pre-Columbian population density was calculated to have been 14.6 persons per km^2, while the upland (*terra firme*) has an estimate of 0.2 persons per km^2 (Denevan 1970). There are indications that populations were clustered, indicating spatial heterogeneity across the landscape (Meggers 1971, Roosevelt 1991, Heckenberger et al. 2003*b*). The upland areas may also have contained numerous large population centers interconnected by roadways (Heckenberger et al. 2003*b*). Estimates of the area of forest altered by pre-Columbian humans span a wide range. It has been estimated that 50% of forest area has been altered in upland areas adjacent to the major rivers, while others suggest 11.8% has been impacted in all of the non-flooded areas (Balée 1989). These estimates rely heavily on the type of agricultural practices assumed to be used to support the resident population (Meggers 1954, Roosevelt 1991, Neves 1999).

The uncertainty over initial human population size and how these populations impact the tropical forest structure and processes also translates into disparate opinions on their legacy effects. If abandonment took place ~1600, there have been only one to three tree generations, and so successional signatures might well still be apparent. One path taken to identify legacy impacts of past human disturbance on forest composition is to document useful tree species, and where an elevated occurrence of useful species suggests a legacy of prior disturbance (Piperno et al. 2015). Such classification of useful species is highly subjective. It is also not known whether such an elevated density of useful species was the result of pre-Columbian activity or more recent, for example, rubber boom, impacts (ter Steege et al. 2013) or merely the result of natural processes or a combination of natural and anthropogenic factors. Recent work has indicated that regions around archaeological sites have different tree species composition than that of nearby forests (Levis et al. 2017).

The typically poor soils of Amazonia, which are mostly severely weathered and nutrient-poor ultisols or oxisols (Quesada et al. 2011), were seen to be a major impediment to the establishment of large, dense, and sedentary populations (Meggers 1971). The realization that highly productive and stable anthropic soils were produced by ancient indigenous populations changed the debate over the Amazonian past (Woods and McCann 1999, Glaser et al. 2001, Petersen et al. 2001). Amazonian Dark Earths (ADEs) or in Portuguese, terras pretas (Smith 1980, Petersen et al. 2001), are anthrosols characterized by high levels of organic matter, charcoal, and nutrient elements (Woods 2003). Frequently associated with large accumulations of potsherds, lithics, and features such as mounds or ditches (Costa et al. 2004, Glaser et al. 2004), these soils were formed over a few generations by sedentary populations with intensive land use and agroforestry management practices (Heckenberger et al. 2003*a*, *b*, Glaser and Birk 2012, Denevan 2014, Neves et al. 2014). Such anthrosols developed as the result of trash middens accumulating beside houses (Medina 1934, Schmidt et al. 2014). Radiometric ^{14}C dating suggests that ADE formed in some locations as long ago as 6000 cal yr BP, but the majority of them were formed between c. 2500 and 1200 cal yr BP (Neves et al. 2014), that is, prior to European contact (Woods 2003). Many ADE sites are found on prominent high bluffs overlooking major rivers such as the Tapajos River near Santarem, where the earliest European travelers in the region reported high indigenous population densities (Denevan 2001, Glaser and Birk 2012). Although hundreds of ADE sites have been reported (German 2004, Kern et al. 2004, Neves and Petersen 2006, WinklerPrins and Aldrich 2010), only recently have comprehensive surveys attempted to document the frequency of occurrence of ADE across Amazonia, specifically in upland forested areas (WinklerPrins and Aldrich 2010, McMichael et al. 2012*b*, Urrego et al. 2013). Quantification of the frequency and spatial distribution of ADE is an important step toward reducing the uncertainty over the pre-Columbian human population and its influence on the evolution of Amazonian forests.

Although many ADE locations are well known, it has been hypothesized that many more exist that have yet to be identified. The quest to map ADE locations has been stymied by the immense size of Amazonia, remoteness of many areas, dense forest, and lack of archaeological field surveys. Remote sensing offers a new opportunity to augment traditional archaeological studies and to contribute to the mapping of ADE soils (Erickson 1995, McGovern 1995, Palace et al. 2008, McMichael et al. 2014*a*). Remote sensing allows for comparison and analysis of vegetation characteristics across vast areas (Palace et al. 2008, Treuhaft et al. 2015). Differences in leaf pigment composition and concentrations can be detectable via optical remote sensing by analysis of multiple wavelengths of the electromagnetic spectrum represented as different reflectance bands (Ustin et al. 2004, Pellissier et al. 2015).

If ADEs can be detected from space, the ecological characteristics and responses to climate forcing can be evaluated on an unprecedented scale. Leaf or foliar chemistry is correlated with soil nutrient concentrations (Martin and Aber 1997), and this difference is detectable using remotely sensed image data (Nicotra et al. 2003). Soil nutrient availability directly affects plant physiological functions, such as photosynthesis, and the development of metabolic and structural molecules (Marschner 1995, Aber and Melillo 2001). Specific wavelength bands are associated with different vegetation characteristics and structure (Chambers et al. 2007). This very discrepancy in nutrient availability in ADE and non-ADE soils lies at the heart of our remote-sensing analysis.

Here, we examine the potential of using moderate spatial resolution optical satellite imagery to estimate the spatial extent of ADE across the entire Amazon Basin. We ask three basic questions: (1) Can ADE soils be reliably detected using remote sensing? (2) What is the spatial distribution of ADE sites in Amazonia forests? (3) What are the biometric characteristics of forests on ADE sites indicating potential impacts of pre-Columbian populations of the forest?

METHODS

Amazonian Dark Earth sites

Our region of study is the Amazon Basin in South America, with the inset map covering an area of high ADE probability (Fig. 1). The locations of ADE sites were extracted from a compilation of existing online sources, published papers, and locations provided by E. Tamanaha (*personal communication*), E. Neves (*personal communication*), and WinklerPrins and Aldrich (2010). Sites were excluded that were not previously classified as having high to medium confidence in accuracy in their geographic coordinates or that lacked coordinates taken using a global positioning system device (WinklerPrins and Aldrich 2010, McMichael et al. 2012*a*). Some sites in both western and eastern Amazonia were excluded due to disturbance, as we were examining intact forests, not recently impacted by humans.

The ADE locations used in our study are primarily located near rivers and clustered in central and eastern Amazonia. These areas have been suggested to be more heavily surveyed by archaeological research and present a bias in sampling. Survey work by archaeologists has attempted to address this issue with carefully planned surveys and sampling parameters. Our use of multiple sources is an effort to include as many potential sites and sampling schemes in an effort to address such as bias. In addition, maximum entropy modeling has been suggested to be less sensitive to sampling location biases than other statistical methods (McMichael et al. 2014*a*).

To examine the spectral signatures of forested ADE sites and relate them to ancient human activity, we had to further filter out sites that were currently non-forested. Thus, we generated a forest filter MODIS 1-km Vegetation Continuous Fields product (MOD44B), using year 2010. We filtered

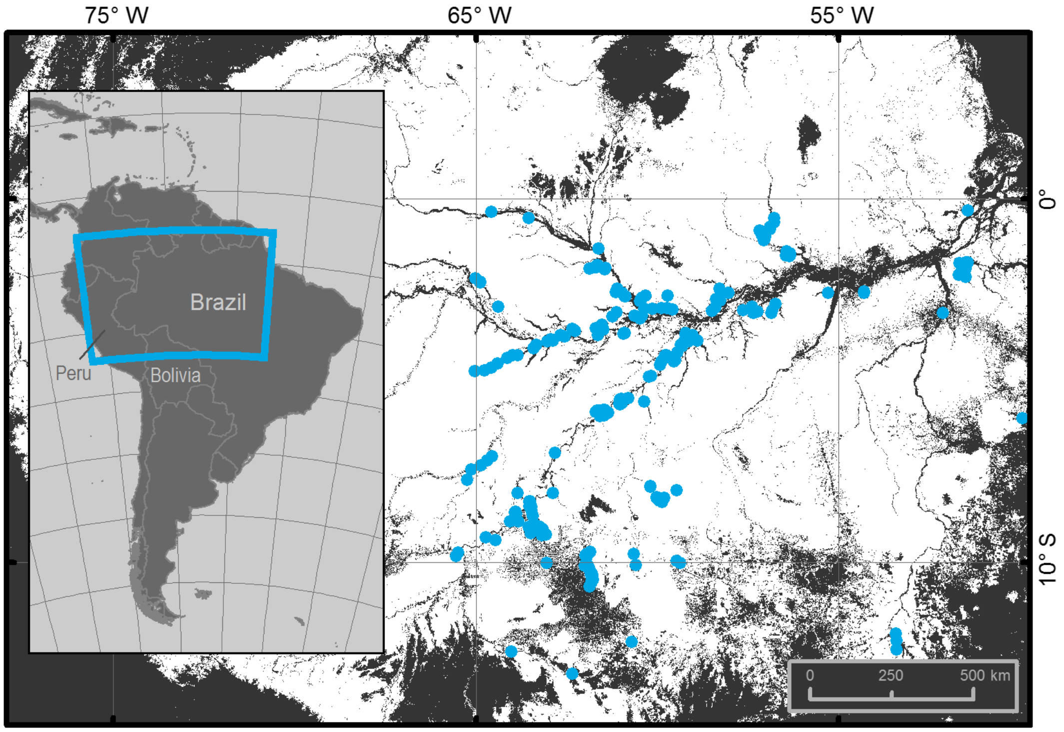

Fig. 1. Location of Amazonian Dark Earth sites (blue dots) and the study area of the analyses. Black areas are regions masked from inclusion in our analysis due low biomass or non-forested areas. The masked area also includes the main stem of the Amazon and some flooded areas.

out sites that had <50% tree cover at the MODIS pixel level. In addition, we used two biomass maps (Saatchi et al. 2007, 2011) to exclude any sites with aboveground biomass <100 Mg/ha. This acted as a further check to increase the likelihood that we were examining only forests not recovery from recent disturbance. A total of 251 ADE locations were used in our analyses, out of the total of 917 from McMichael et al. (2014*a*), indicating that 72% of known ADE sites are located on cleared land under cultivation or in secondary forests. The geographical distribution of the included 28% of the ADE sites was similar to the distribution of the sites used by McMichael et al. (2014*a*). Amazonian Dark Earth sites have been shown to be larger than two hectares and at times greater than fifteen hectares (Costa et al. 2004). Others have suggested that ADE sites may extend over several square kilometers (Sombroek et al. 2002). Our effort was to examine whether the MODIS 500-m spatial resolution (25 ha) was sufficient for identification of ADE sites. Fifty random points were generated within 50 km for each ADE site. These random points adhered to the same forest cover and biomass criteria we set for inclusion of ADE sites in our study and were also not known to be ADE sites. These random points were generated for comparison of the spectral differences between ADE and randomly selected sites and are assumed to not contain ADE. A total of 12,550 random points were used in comparison with the 251 ADE sites.

Moderate spatial resolution optical satellite imagery extraction indices

Moderate spatial resolution optical satellite imagery provides the best available platform to image tropical forests over large regions, and due to repeat coverage, issues of cloudiness can be addressed. Temporal resolution of image capture ranges from 1 to 8 d, and spatial resolution spans from 250 to 1000 km. A total of 36 spectral reflectance bands (ranging from 620 nm to 1.385 μm) are collected by MODIS and are used to develop data products that include the characterization of terrestrial vegetation and atmospheric properties (Justice et al. 1998, Hagen et al. 2002, Braswell et al. 2003). Leaf pigments from the top of canopy tend to be reflected in the visible spectrum (400–700 nm) while the canopy water content is found to reflect in the near-IR spectrum (700–1300 nm; Chambers et al. 2007). We note that MODIS land optical bands only extend to 2.7 μm, but contain bands that allow for examination of leaf pigments and canopy water.

Moderate spatial resolution optical satellite imagery data were used in both our maximum entropy modeling and our comparison of ADE and random forested sites. We used four indices derived from the MODIS nadir-bidirectional reflectance distribution function (BRDF) adjusted reflectance (MCD44A4) product, and four dry season months for the years 2004, 2005, 2009, and 2010. These indices are ratios between spectral bands that focus on specific aspects of forest canopy properties. The normalized difference vegetation index (NDVI) is a measure of the density of greenness in a pixel. The land surface water index (LSWI) provides a measure of the hydration of both soil and vegetation. The visible atmospherically resistance index (VARI) is another metric providing a proxy measure for greenness. The brightness (BRGT) index is a proxy for the total albedo of the pixel.

We used the MODIS nadir-BRDF adjusted reflectance product (MCD43A4). BRDF is defined as the bidirectional reflectance distribution function, which examines how light is reflected from a surface and how such angles and reflections. Influences on forest canopies on the reflected light can be considerable (Morton et al. 2014). The MCD43A4 MODIS product accounts for the bidirectional influence. We extracted the reflectance values of this product for each of the ADE and non-ADE sites, including values for four dry season months (June–September) for the years 2004, 2005, 2009, and 2010. Strong droughts occurred in Amazonia in 2005 and 2010. The 2005 drought was stronger west of 66° W and weaker east of 66° W (Frolking et al. 2011, 2017), coinciding with where known ADE sites are located across the west to east portion of Amazonia. We included these drought years because differences in the forest canopy reflective properties might be enhanced under dry conditions. In addition, these four months generally represent the dry season across much of the basin and have proportionally more cloud-free and uncontaminated pixels. The resolution of imagery used was 500 m. The four indices that we calculated were NDVI, LSWI, VARI, and BRGT:

$$\mathrm{NDVI} = \frac{\mathrm{nir} - \mathrm{red}}{\mathrm{nir} + \mathrm{red}} \quad (1)$$

$$\mathrm{LSWI} = \frac{\mathrm{nir} - \mathrm{mir}}{\mathrm{nir} + \mathrm{mir}} \quad (2)$$

$$\mathrm{VARI} = \frac{(\mathrm{green} - \mathrm{red})}{(\mathrm{green} + \mathrm{red} - \mathrm{blue})} \quad (3)$$

$$\begin{aligned}\mathrm{BRGT} &= 0.3 \times \mathrm{blue} + 0.3 \times \mathrm{red} \\ &\quad + 0.3 \times \mathrm{green} + 0.1 \times \mathrm{nir}\end{aligned} \quad (4)$$

where blue is MODIS band 3 (459–479 nm), green is band 4 (545–565 nm), red is band 1 (620–670 nm), nir is band 2 (841–876 nm), and mir is band 6 (1628–1652 nm). Of the four indices, NDVI is the most widely known and has been shown to be related to vegetation density, canopy cover fraction, photosynthesis rates, net primary productivity, and other aspects of plant activity, depending on the time and spatial scale examined (Petorelli et al. 2005). The LSWI is functionally similar to NDVI but takes advantage of the relatively stronger scattering of leaf water in the mid-infrared relative to near infrared (Chandrasekar et al. 2010, Gamon et al. 2016). LSWI uses the channel 6 mid-range infrared (MIR) which has been suggested to be a more robust option than using channel 7 MIR. The VARI (Gitelson et al. 2002) is meant to be sensitive specifically to the strength of absorption of chlorophyll b in the red band relative to the green band, with an additional adjustment factor using the blue band to account for atmospheric effects (Appendix S1: Fig. S1). BRGT is not a vegetation index, but simply a proxy for albedo, with broad MODIS bands weighted to account for the approximate strength of incoming solar radiation in the respective bands.

Choosing indices to use in analysis

We generated a total of 64 potential variables for use in our modeling efforts (four years, four months, four indices). In an effort to reduce the large number of potential environmental layers or variables going into a geospatial model, we conducted *t* tests on each index/year/month, comparing known ADE sites and random sites. We selected the 10 spatial layers that showed the greatest contrast (i.e., with lowest *P*-value from *t* tests; Table 1; Appendix S1: Fig. S1) between ADE sites and randomly selected sites. The top two selected layers were VARI in September for 2005 and 2009 (Appendix S1: Fig. S1).

Table 1. Results indicating the importance of the top 10 variables in the development of a prediction model indicated by permutation importance and sorted by lowest *P* value from *t* tests.

Index	Month	Year	Permutation importance
Visible atmospherically resistant index (VARI)	September	2009	14.6
VARI	September	2010	13.9
Land surface water index (LSWI)	September	2005	2.9
Normalized difference vegetation index (NDVI)	August	2009	30.2
LSWI	September	2010	2
NDVI	September	2009	11.4
VARI	August	2009	10.5
VARI	September	2005	3
NDVI	September	2010	8.3
NDVI	September	2005	3.2

Geospatial processing and statistical analysis

Organization of ADE sites, MODIS monthly averages, and reflective index calculations were all done in Python 2.7. Extraction of points for statistical analysis, graphing, and mapping was performed with QGIS 2.14 Essen. We used MaxEnt modeling software version 3.3.3 (Philips et al. 2006) to generate predictive models of ADE across Amazonia using MODIS values as predictors and ADE locations as occurrence points. We applied the same forest mask to all MODIS datasets for use in our spatial predictive modeling. Ten covariates were used as environmental or spatial layers in our modeling effort. We ran our model with *k*-fold cross-validations. Iterations were run using a convergence threshold set at 0.0001 and with a default prevalence of 0.5. Response curves were generated for each input variable in our MaxEnt model. Jackknife tests were run to examine the importance, or relative contribution, of each variable to the model, both when the variable was used exclusively to build the model and when it is excluded from the model (Howey et al. 2016). Jackknife tests were done for both training and test datasets. The contribution of a specific variable is estimated based on the regularized gain observed when the variable is included in the model (Table 1). Response curves were developed for each variable (Appendix S1: Figs. S2, S3). The area under the curve (AUC) statistic was used to gauge the predictive capacity of our model and how well it performed compared with a null model. Area under the curve values from a model greater than 0.75 are considered to predict the test point distribution accurately (McMichael et al. 2014*a*). All statistical analyses were performed in JMP Pro 12 and graphs were generated using SigmaPlot 10 (Systat Software, Inc., San Jose, California, USA). Biometric properties from forested regions in the Amazon were examined for comparison between ADE and random sites. Data sources used are presented in Table 2.

Impact of ADE on tropical forest structure

Once a probability map was developed of ADE distribution across the basin, we were interested in the impact that indigenous people and ADE sites might have on the tropical forest biometry. First, we examined the differences between ADE sites and random sites for biomass, forest height, percent tree cover, and distance to forest edge. We used previously generated data products for this effort, which included biomass (Saatchi et al. 2011, Baccini et al. 2012, Avitabile et al. 2016), forest height (Simard et al. 2011), percent tree cover (Hansen et al. 2013), and our estimate using our non-forest mask (distance to edge of forest; Appendix S1: Fig. S4). We developed spatial impact maps using the average difference in biomass and estimated ADE probability from our MaxEnt modeling effort. A simple formula representing biomass reduction was developed:

$$\Delta B = P_{\mathrm{MaxEnt}} \cdot B \cdot \delta B_{\mathrm{ADE}}$$

where ΔB is the change in aboveground biomass (Mg/ha), P_{MaxEnt} is the probability of a ADE site from the MaxEnt model, B is the aboveground biomass (Mg/ha), and δB_{ADE} is the mean aboveground biomass reduction as a fraction of total biomass for a pixel. We were interested in mapping the potential increase or decrease in aboveground biomass as an extension of anthropogenic past disturbance through the region.

RESULTS

MODIS ADE vs. random site indices

Monthly averages for MODIS indices were different between ADE sites and randomly selected sites (Fig. 2). In most cases, differences between years and between ADE and random site data increased as the dry season progressed (and water stress probably increased) from June through September (Fig. 2). Normalized difference vegetation index values were lower for ADE sites later in the dry season (August and September) for both drought years (2005 and 2009) and normal years (2004, 2010) compared with random sites; however, 2009 and 2010 showed greater variation (Fig. 2). Land surface water index was lower for both ADE sites and random sites during the drought years with greater differences between 2009 and 2010 (Fig. 2). Amazonian Dark Earth sites had lower VARI values than random sites for all months and for both 2004 and 2005, though VARI values were lower for ADE sites in 2005 and 2009 compared with 2004 and 2010, respectively (Fig. 2). VARI showed little difference between ADE sites and random sites for all months for 2004 and 2005. For VARI in 2009 and 2010, the differences between ADE and random sites were greatest in August and September, with the differences primarily between years and not between ADE and random sites (Fig. 2). BRGT showed an increase over the four-month time period for both ADE sites and random sites.

Table 2. Biometric properties and distance from edge for Amazonian Dark Earth (ADE) and random sites.

Forest biometric properties	ADE	Random	Summary	Source
Biomass (Mg/ha)	206.3 ± 32.9	211.6 ± 33.7	<0.0421	Saatchi et al. (2011)
Biomass (Mg/ha)	227.8 ± 92.0	254.0 ± 57.2	<0.0001	Baccini et al. (2012)
Biomass (Mg/ha)	210.9 ± 65.8	222.7 ± 73.7	0.01	Avitabile et al. (2016)
Tree height (m)	27.4 ± 6.3	29.4 ± 5.4	<0.0001	Simard et al. (2011)
Percent cover	91.6 ± 12.3	97.8 ± 6.6	<0.0001	Hansen et al. (2013)
Distance from edge (km)	4.8 ± 12.1	6.2 ± 12.1	N.S.	Non-forest mask

Notes: N.S., not significant. Values are mean followed by standard deviation.

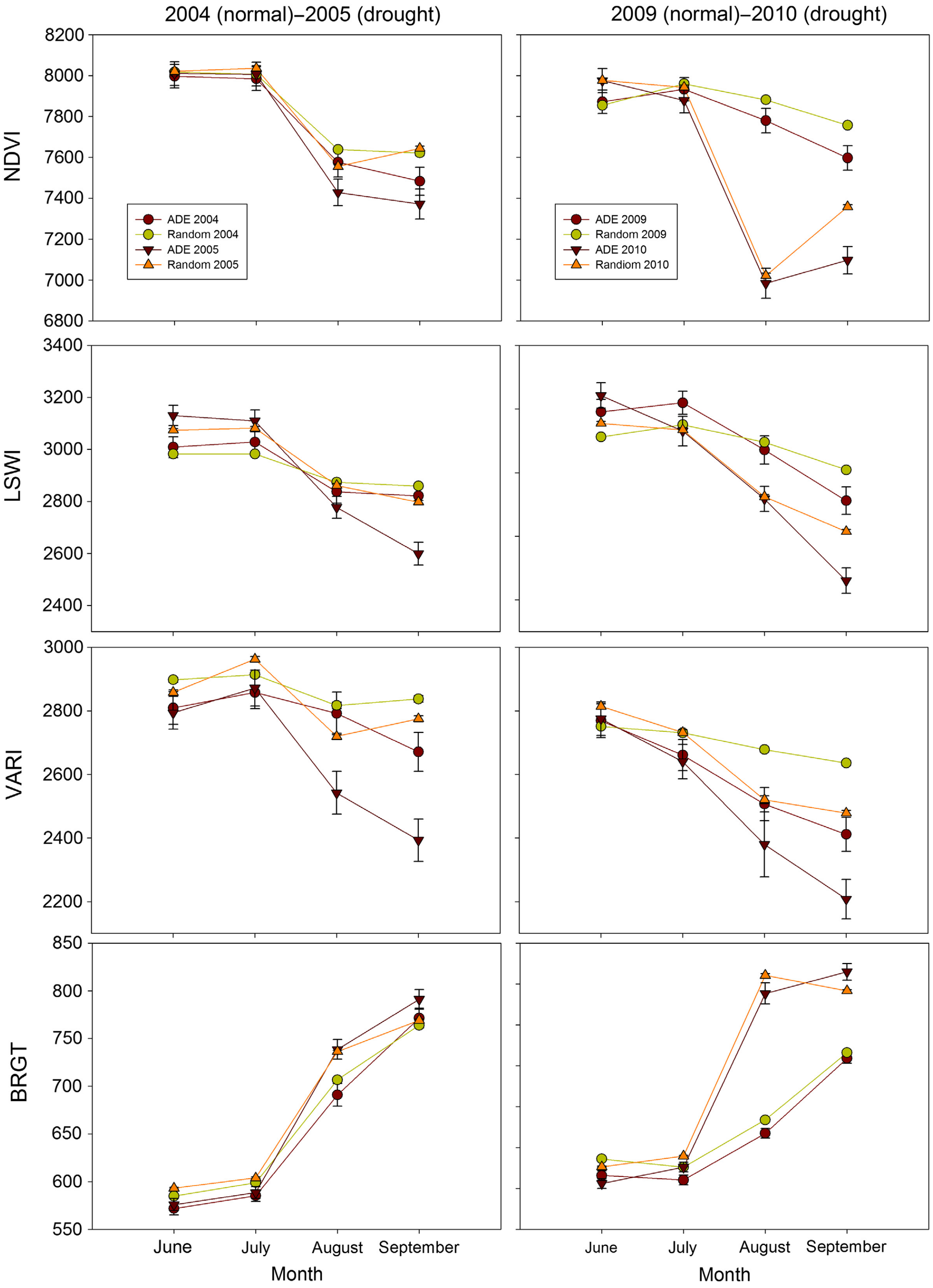

Fig. 2. Four indices used in our analysis for four months in 2004 and 2005 (left) and four months in 2009 and

(Fig. 2. *Continued*)
2010 (right), comparing Amazonian Dark Earth (ADE) sites and random sites near each of the ADE sites. Circles represent non-drought years. Triangles represent drought years. Red colors represent ADE sites. NDVI, normalized difference vegetation index; LSWI, land surface water index; VARI, visible atmospheric resistance index.

Geospatial model

A map of ADE likelihood was generated across the region using MaxEnt modeling (Fig. 3). We only used known ADE sites in the maximum entropy modeling. The average test, or out-of-sample, AUC value for the replicate runs was 0.791, with a standard deviation of 0.261, which indicated that the model performed well and was able to predict the test data accurately.

The results for the jackknife test, using AUC on test data, to examine the importance of individual variables indicated that the variable with highest gain when used in isolation is VARI in September 2010 (0.6523 AUC) and thus may be considered the variable with the most useful individual information. Visible atmospherically resistance index in August 2009 (0.7131 AUC) is the variable that reduces the gain the most when excluded from the model, thus indicating that this variable has the most useful unique information in comparison with other variables.

The variable with the highest permutation importance was NDVI August 2009, at 30.2%. The second highest permutation importance variable was VARI September 2009. The permutation importance is the value of that variable to the model contribution when all other variables are held constant. The response curves for each individual variable averaged over the runs are presented in the supplemental material (Appendix S1: Figs. S3, S4).

Biometric properties between ADE vs. random sites

Using the probability map of ADE sites and an estimate of the average biomass reduction on ADE

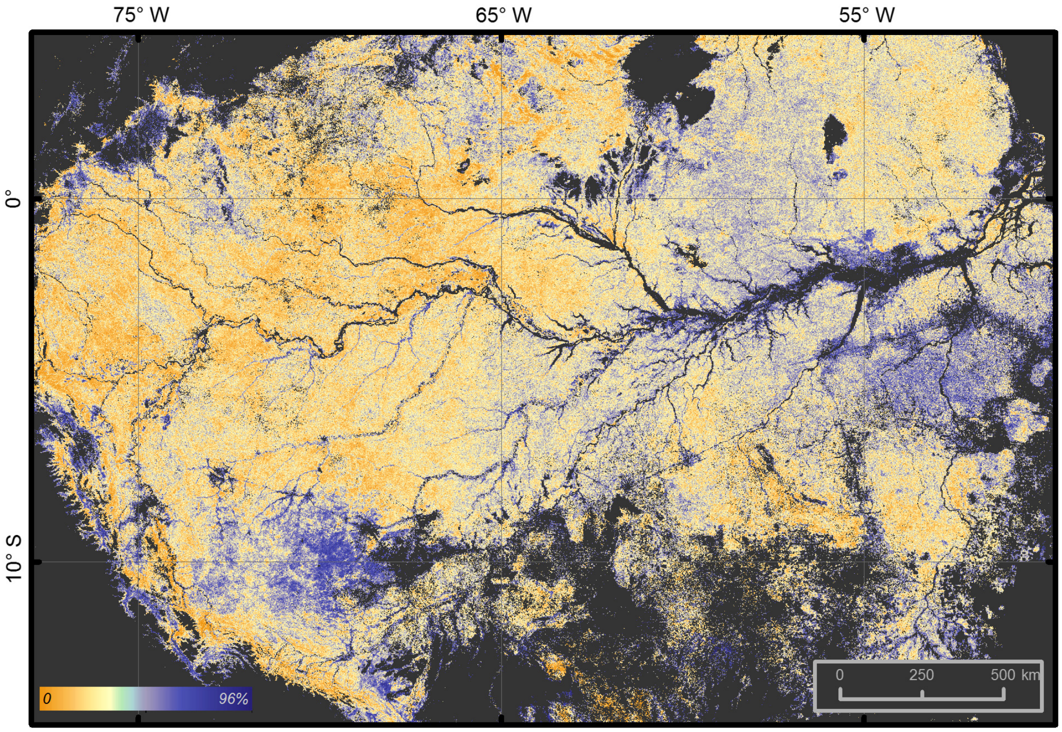

Fig. 3. Prediction of Amazonian Dark Earth across Amazonia using MaxEnt modeling. The black area is a non-forest mask or was not included in our analysis due to clouds or instrument errors of the satellite platform.

sites, we provide an estimate of the anthropogenic forcing of pre-Columbian populations on Amazonian forests**.** We compared biometric properties using existing data sources to examine whether the optical differences in MODIS indices were correlated with forest structure. These included biomass (Saatchi et al. 2011, Baccini et al. 2012, Avitabile et al. 2016), forest height (Simard et al. 2011), percent tree cover (Hansen et al. 2013), and our estimate using our non-forest mask (distance to edge of forest; Appendix S1: Fig. S4). We found that biomass, tree height, and percent tree cover were all significantly lower at ADE sites compared to random sites (Table 2). Biomass was 8.2% lower on ADE sites, using the biomass values from Baccini et al. (2012). There was a 10% decrease in the average tree height on ADE sites compared to random forested sites. Percent tree cover was 9.0% lower on ADE sites also when compared to random forested sites. To test whether ADE sites may be impacted by degradation or used for extractive resources, we compared the distance from edge of cleared land or secondary forest. We found no difference in the distance from the edge of non-forested areas and ADE and random sites.

Discussion

Can ADE sites be detected using remote sensing?

Recently, researchers used Spot6 image data (1.5 m) to examine ADE distribution in agricultural fields tens of kilometers with promising results (Söderström et al. 2016). Agricultural fields vary tremendously based on the recent history of land use, and applying such a methodology with very high-resolution data across larger regions can be difficult. We used MODIS (MCD44B) indices generated in the dry seasons of 2004, 2005, 2009, and 2010, to assess whether known ADE sites could be predicted across the Amazonian region for intact forests. Using different indices derived from MODIS, our model robustly predicted the ADE sites in the testing dataset (AUC of test data = 0.791; Fig. 3). In addition, our analysis showed that ADE forest sites differ spectrally from randomly located forested sites adjacent to known ADE sites.

In general, the dry season in Amazonia is from June through September, with some northern areas of Amazonia having a slight temporal shift due to the movement of the Intertropical Convergence Zone. During the months from June through September, BRGT (a proxy for albedo) from the ADE sites increased more than that of the non-ADE sites, while NDVI, LWSI, and VARI (photosynthesis index) decreased. This finding suggested that the forests of ADE sites had fewer green leaves, were less photosynthetically active, and had drier canopies. This result was not consistent with our initial expectation that the greater nutrient availability common to ADE soils would result in more robust drought resistance. At one forested site in the eastern Amazon, researchers found that Net Primary Productivity (NPP) fell dramatically during the dry season on an ADE site when compared with a non-ADE site (Doughty et al. 2014). Several different explanations for such differences in spectral indices can be proposed that are not mutually exclusive or that may apply more in one location than another. The species composition on ADE soils may simply be different to that of non-ADE soils (Junqueira et al. 2011), resulting in different reflectance as they become stressed with progression of the dry season. The relative resource allocation to root depth on differing soil types is largely unknown for Amazonian trees and could be an important determinant of drought resistance (Asner and Vitousek 2005). Seedling recruitment has been shown to be lower on ADE sites and was attributed to Ca toxicity and nutrient imbalances (Quintero-Vallejo et al. 2015), and this could contribute to differences in species composition. Others have suggested that ADE abandonment resulted in mineralization of organic C and nutrient leaching, thus reducing overall nutrient content and humus in the soil and potentially influencing forest structure (Neves et al. 2004). We suggest that differences in root mats, soil moisture, and seedling recruitment may also be driving factors.

What is the spatial distribution of ADE sites across Amazonia?

Our findings indicate that forests on ADE sites are more susceptible to drought. Clearing a tropical forest without metal axes is difficult; indigenous people could have used slash and burn, and/or slash and char, using fire to aid in the conversion of forest to intensive agroforestry systems (Arroyo-Kalin 2012). Thus, it seems intuitive that ADE sites may have been pre-selected to lie in regions that were readily burned due to the propensity for drought or intensity of dry seasons. Once ADEs developed, they became areas of interest for groups and potentially for further reoccupation.

Our results highlighted the prevalence of ADE sites along the main rivers in Amazonia, particularly in the central and eastern regions, which agrees with a geospatial model that used the occurrence points with climatic, geological, and geographical predictors (McMichael et al. 2014*a*). Both models have predicted high spatial heterogeneity in ADE sites across the Amazon and suggest that the overall picture of pre-Columbian occupation by indigenous people is complex. Ancient people likely were attracted to specific environmental parameters often that have a spatial component (e.g., topography, distance to rivers, or biome type), to construct settlements and grow crops. Each of these modeled predictive maps, our current study and McMichael et al. (2014*a*), is independent, and the locations of ADE sites are essentially the same. In our current study, we had fewer ADE sites, due to filtering out sites that lacked a modern intact forest. To leverage the strength of each of these datasets, we averaged the two predictive model maps (Fig. 4). Each of these independently derived models, within a Bayesian framework, represents an equally likely prediction and thus can be combined with equal weights. The concordance between the two models is striking along rivers and in the low density of ADE sites predicted in western Amazonia.

Such a focus on unique environmental variables has also been shown in other archaeological studies using predictive modeling (Neves et al. 2004, McMichael et al. 2012*a*, *b*, Bovin et al. 2016, Howey et al. 2016). The specific environmental preferences and cultural patterns of ancient people, however, might have also varied across the vastness of Amazonia (McMichael et al. 2012*a*, *b*). Within central and eastern Amazonia, our study documented the preference of ancient people to enhance soils and live near rivers, where fish provided the highest resource base in the region (Prestes-Carneiro et al. 2016). In southwestern Amazonia, geospatial models have shown that

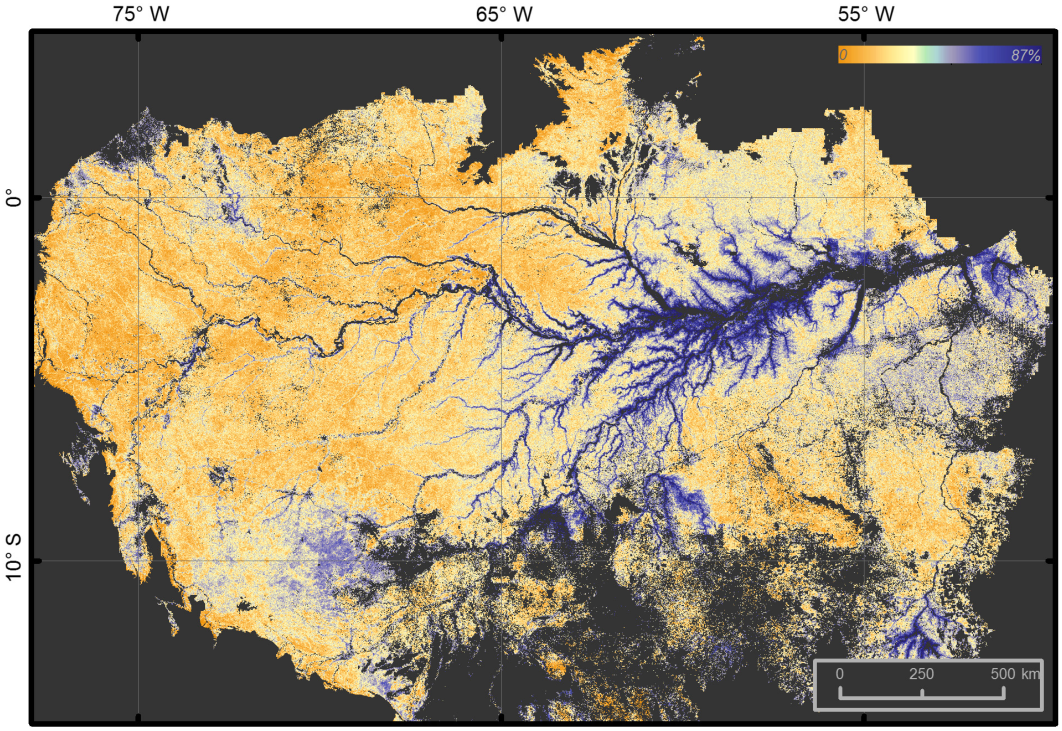

Fig. 4. Average probability map using moderate spatial resolution optical satellite imagery based MaxEnt model (Fig. 3) and McMichael et al. (2014*a*).

earthwork construction replaced ADE formation and appears to have been associated with bamboo-dominated systems (McMichael et al. 2014*a*, *b*). Our probability map of ADE sites could prove useful for the planning of future surveys and sampling schemes for archaeological and ecological research.

Are ADE properties a legacy of pre-Columbian disturbance?

Quantitative assessments of biomass, forest diversity, species clumping, tree age structure, and epiphyte load have not been used to make the case for legacy effects of pre-Columbian activity, yet all could be argued to be viable signals of past human actions. Junquira et al. (2011) found higher palm abundances on ADE sites. Biomass, tree height, and percent tree cover are all lower at ADE than random non-ADE sites, which may be due to differences in tree species, ecosystem processes, and other attributes of forest structure. Differences between ADE sites and non-ADE site for tree height and biomass have been shown by Doughty et al. (2014), but we note that the ADE plot in that study had also been selectively logged. There was no difference in distance from forest edge between ADE and random sites, indicating that any differences are likely not due to recent forest degradation, logging, or intrusion of people into these forests based on distance alone. Three basic explanations could account for the biometric structural differences between ADE and non-ADE forests: (1) The ADE sites may be regrowth forest from sites cleared prior to abandonment, with the successional path of these forests following a unique trajectory; (2) these may be remnant forests that were altered in terms of composition and structure by human action prior to European Conquest and have continued to be used (albeit perhaps differently) in the centuries since; and (3) as in 2, but that have not been used throughout the last 400 years.

Antony and van Roy (2002) and Junqueira and Clement (2011) suggest differences in biodiversity between ADE sites and surrounding areas. Because palms were an important resource used systematically by indigenous people since the beginning of the Holocene (Morcote-Ríos and Bernal 2001), it is possible that palms are more common on ADE sites than in non-ADE forests (Neves et al. 2004). Such a propensity of palm biomass on ADE sites may result in differences in forest spectral properties, for example, lower biomass, fuller subcanopy, or fewer canopy emergents. Furthermore, Levis et al. (2017) describe an influence of archaeological sites on the biodiversity. They find that areas adjacent to archaeological sites may be anthropogenic forests from past societies, meaning that these forests are a result of tree species and structure encouraged for growth or manipulation to promote extractable forest resources. The spectral properties from our MODIS analysis indicate these differences in forest structure. Our examination of ADE and random site biometric properties reveals structural differences between the two (Table 2). The model appears to key in on forested areas in which ADEs have different vegetation structure and possibly species. This finding is contrary to our initial expectation that relative to non-ADE settings, ADE sites with nutrient-rich soils would have healthier trees with higher foliar nutrient content (Martin and Aber 1997, Pellissier et al. 2015, Lepine et al. 2016). We suggest that the differences in spectral properties may be due to differences in both forest structure and tree species, which indicate long-term impacts from past human settlement patterns. In essence, these are anthropogenic forests.

Our results suggest that remotely sensed data have the capabilities of capturing past disturbances, possibly even pre-Columbian disturbances, on a basin-wide scale. Our results facilitate incorporation of past disturbances into studies of modern forest patterns and processes. For example, distributions of particular forest species may be related to the distribution of ancient disturbances (Junqueira et al. 2011, McMichael et al. 2012*a*, *b*, 2015, 2017, ter Steege et al. 2013, Bush et al. 2016). Using a minimum value as a cutoff for both biomass and percent forest cover, we masked out early-successional forests. Some areas that were predicted to have high ADE probabilities appear to be adjacent to some of the modern deforestation in Pará, even though the mask was restrictive and distance from edge is no different between ADE and random sites. These deforested areas may be ADEs selected by modern settlers for their enhanced soils. We also suggest that our use of remote-sensing data might not just be keying in on ADE sites, but other forest impacts by pre-Columbian societies as they manipulated forests. The large urban arrangements suggested by Heckenberger et al. (2008) would have needed fuelwood as a resource. Such extraction of fuelwood would have expanded its center of influence outward. Though ADE sites may be centered on occupation areas, our findings of reduced biomass and tree height may well be indicative of degraded forests from past peoples around high population centers.

Using the probability map of ADE sites and an average biomass reduction, we provide an estimate of the anthropogenic forcing of pre-Columbian populations on Amazonian forests. If we assume a mean reduction of biomass of 2.0 Mg/ha and weight the amount based on the probability of the area being modified by human activity (Fig. 4; Appendix S1: Table S1), we estimate that contemporary forest carbon storage is reduced by 1.2 Pg across the basin or about 1% of total carbon stored in vegetation (Tian et al. 2000; Fig. 5). This is a one-time reduction of biomass. We note that this estimate of biomass reduction is well within the error estimate of regional biomass products (Saatchi et al. 2011, Baccini et al. 2012). What we point out is that proposed reduction in biomass may also be a representation of what biomass would be like at these sites based on other climatic and biotic controls (Tian et al. 2000). Estimates of regeneration and carbon sequestration, though considerable, are much lower than our estimate of reduced biomass potential due to pre-Columbian populations on Amazonian forest (Nevle et al. 2011). We suggest future research effort to focus on the reduction of error in biomass estimates across Amazonia.

The previously published geospatial models in Amazonia have robustly documented the likely distribution of ancient people across the landscape (McMichael et al. 2014*a*, *b*). These models, however, are unable to link those distributions with characteristics observed in the modern forest. Our results provide the first empirical data that links ancient disturbance to modern forest reflectance values. Whether there has been ongoing disturbance that has intermittently or continuously shaped these forests since the time of European Conquest remains to be determined. Our methods could also be used to examine the legacies of ancient human impacts on the

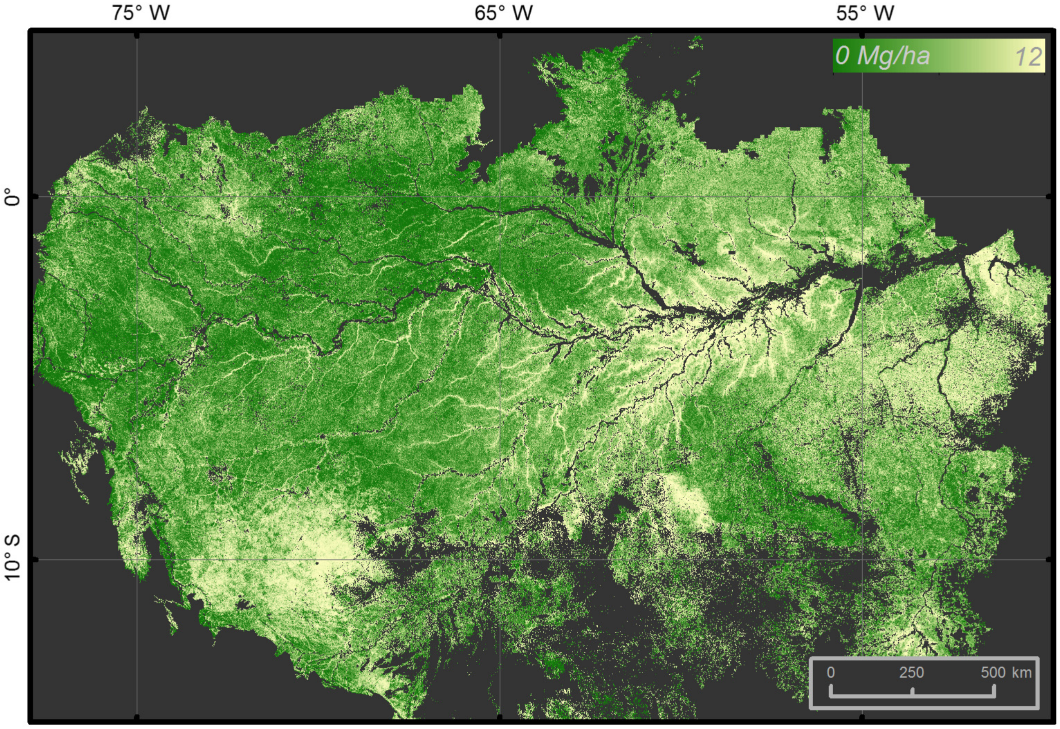

Fig. 5. Predicted biomass reduction across the region based on the Amazonian Dark Earth site distribution and lower biomass on these sites.

landscape across other geographic regions, given a solid knowledge of the forest structure and ecology of the modern system.

Our finding suggests that ancient Amazonian populations left lasting impacts on forest structure. Such an impact needs to be considered when interpreting and analyzing modern ecological studies. Our study also suggests that the response of ADE sites to droughts is different than non-ADE sites, further indicating an ecological nuance potentially missed in ecological literature. The potential for differences in structure, species composition, and ecological processes needs to be noted by the ecological community.

Conclusions

Amazonian Dark Earths are an anthropic soil with enriched nutrient levels and a prime indicator of past human activity in this region. We used satellite imagery and geospatial modeling to predict the ADE probability across the 6 million km^2 of Amazonia. Our satellite-based efforts show that ADEs can be detected from space as the modern forests growing on the anthrosols are more susceptible to drought than neighboring non-ADE sites. Our study found that ADE sites had lower VARI, NDVI, and LSWI values than random sites. Such differences were more pronounced in the two years that experienced drought. This finding is contrary to the expectation that ADE sites with nutrient-rich soils harbor healthier trees with a higher canopy hydration state, as expressed by canopy reflectance. We suggest that ADE sites have different effective water loss due to soil properties, tree species and structure, and root dynamics of these trees. We found differences in biomass and tree height when comparing ADE sites and random sites. Our findings suggested that pre-Columbian human activity is measurable in Amazonian forest across the region using satellite-based moderate-resolution optical data.

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Literature Cited

Aber, J. D., and J. M. Melillo. 2001. Terrestrial ecosystems. Cengage Learning, Boston, Massachusetts, USA.

Antony, L. M. K. and van Roy V. M. A.. 2002. Invertebrados do solo de Terra Preta Arqueológica no Município de Manacapuru, Amazonas, Brasil *in* Resumos do 19 Congresso Brasileiro de Entomologia, Manuas, 16–21 Junho.

Arroyo-Kalin, M. 2012. Slash-burn-and-churn: landscape history and crop cultivation in pre-Columbian Amazonia. Quaternary International 249:4–18.

Asner, G. P., and P. M. Vitousek. 2005. Remote analysis of biological invasion and biogeochemical change. Proceedings of the National Academy of Sciences 102:4383–4386.

Avitabile, V., et al. 2016. An integrated pan-tropical biomass map using multiple reference datasets. Global Change Biology 22:1406–1420.

Baccini, A., et al. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nature Climate Change 2: 182–185.

Balée, W. L. 1989. The culture of Amazonian forest. Advances in Economic Botany 7:1–21.

Balée, W. L., and C. L. Erickson. 2006. Time and complexity in historical ecology. Pages 1–20 *in* W. L. Balée and C. L. Erickson, editors. Time and complexity in historical ecology: studies in the neotropical lowlands. Columbia University Press, New York, New York, USA.

Betts, R. A., P. M. Cox, M. Collins, P. P. Harris, C. Huntingford, and C. D. Jones. 2004. The role of ecosystem–atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. Theoretical and Applied Climatology 78:157–175.

Bovin, N. L., M. A. Zeder, D. Q. Fuller, A. Crowther, G. Larson, J. M. Erlandson, T. Denham, and M. D. Petraglia. 2016. Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. Proceedings of the National Academy of Sciences of the United States of America 113:6388–6396.

Braswell, B. H., S. Hagen, S. Frolking, and W. A. Salas. 2003. A multivariable approach for mapping subpixel land cover distributions using MISR and MODIS: application in the Brazilian Amazon region. Remote Sensing of Environment 87:243–256.

Brondizio, E. 2003. Revisiting Amazonia Circa 1492, Letters. Science 302:2067–2068.

Brown, I. F., L. A. Martinelli, W. Wayt Thomas, M. Z. Moreira, C. A. Cid Ferreira, and R. A. Victoria. 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. Forest Ecology and Management 75:175–189.

Brugger, S. O., E. Gobel, J. F. N. van Leeuwen, M. P. Ledru, D. Colombaroli, W. O. van der Knapp, and U. Lombardo. 2016. Long-term man–environment interactions in the Bolivian Amazon: 8000 years of vegetation dynamics. Quaternary Science Reviews 132:114–128.

Bush, M. B., A. Correa-Metrio, C. H. McMichael, S. Sully, C. R. Shadik, B. G. Valencia, T. Guilderson, M. Steinitz-Kannan, and J. T. Overpeck. 2016. A 6900-year history of landscape modification by humans in lowland Amazonia. Quaternary Science Reviews 141:52–64.

Bush, M. B., and C. H. McMichael. 2016. Holocene variability of an Amazonian hyperdominant. Journal of Ecology 104:1370–1378.

Bush, M. B., D. R. Piperno, and P. A. Colinvaux. 1989. A 6000-year history of Amazonian maize cultivation. Nature 340:303–305.

Bush, M. B., and M. R. Silman. 2007. Amazonian exploitation revisited: ecological asymmetry and the policy pendulum. Frontiers in Ecology and the Environment 5:457–465.

Bustamante, M. C., et al. 2016. Towards an integrated monitoring framework to assess the effects of tropical forest degradation and recovery on carbon stocks and biodiversity. Global Change Biology 22: 92–109.

Chambers, J. Q., G. P. Asner, D. C. Morton, L. O. Anderson, S. S. Saatchi, F. D. B. Espírito-Santo, M. Palace, and C. Souza Jr. 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. Trends in Ecology & Evolution 22:414–423.

Chambouleyron, R., B. C. Barbosa, F. A. Bombardi, and C. R. Sousa. 2011. 'Formidable contagion': epidemics, work and recruitment in Colonial Amazonia (1660–1750). História, Ciências, Saúde-Manguinhos 18:987–1004.

Chandrasekar, K., M. V. R. S. Sai, P. S. Roy, and R. S. Dwevedi. 2010. Land surface water index (LSWI) response to rainfall and NDVI using MODIS vegetation index product. International Journal of Remote Sensing 31:3987–4005.

Chave, J., B. Riéra, and M. A. Dubois. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. Journal of Tropical Ecology 17:79–96.

Clement, C. R., W. M. Denevan, M. J. Heckenberger, A. B. Junqueira, E. G. Neves, W. G. Teixeira, and W. I. Woods. 2015. The domestication of Amazonia before European conquest. Proceedings of the Royal Society B 282:20150813.

Comas, J. 1951. La realidad del trato dado a los indigenas de America entro los siglos XV y XX. America Indigena 11:323–370.

Costa, M., D. Kern, and N. Kampf. 2004. Pedogeochemical and mineralogical analysis of Amazonian dark earths. Pages 333–351 *in* J. Lehmann, D. Kern, B. Glaser, and W. I. Wood, editors. Amazonian dark earths: origins, properties, management. Springer Science, Dordrecht, The Netherlands.

Crosby, A. W. 2004. Ecological imperialism: the biological expansion of Europe, 900–1900. Cambridge University Press, Cambridge, UK.

Denevan, W. M. 1970. The aboriginal population of western Amazonia in relation to habitat and subsistence. Revista geográfica 72:61–86.

Denevan, W. M. 1992. The aboriginal population of Amazonia. Pages 205–234 *in* W. M. Denevan, editor. The native populations of the Americas in 1492. The University of Wisconsin Press, Madison, Wisconsin, USA.

Denevan, W. M. 2001. Cultivated landscapes of native Amazonia and the Andes. Oxford Press, Oxford, UK.

Denevan, W. M. 2014. Estimating Amazonian Indian numbers in 1492. Journal of Latin American Studies 13:207–221.

Dobyns, H. F. 1966. Estimating Aboriginal American population: an appraisal of techniques with a New Hemispheric estimate. Current Anthropology 7: 395–416.

Doughty, C. E., et al. 2014. The production, allocation, and cycling of carbon in a forest on fertile *terra preta* soil in eastern Amazonia compared with a forest on adjacent infertile soil. Plant Ecology & Diversity 7:41–53.

Erickson, C. 1995. Archaeological methods for the study of ancient landscapes of the Llanos de Mojos in the Bolivian Amazon. Pages 66–95 *in* P. Stahl, editor. Archeology in the lowland American tropics: current analytical methods and applications. Cambridge University Press, Cambridge, UK.

Frolking, S., S. Hagen, B. Braswell, T. Milliman, C. Herrick, S. Peterson, D. Roberts, M. Keller, and M. Palace. 2017. Evaluating multiple causes of persistent low microwave backscatter from Amazon forests after the 2005 drought. PLoS ONE 12:e0183308.

Frolking, S., T. Milliman, M. Palace, D. Wisser, R. Lammers, and M. Fahnestock. 2011. Tropical forest backscatter anomaly evident in SeaWinds scatterometer morning overpass data during 2005 drought in Amazonia. Remote Sensing of Environment 115:897–907.

Gamon, J. A., K. F. Huemmrich, C. Y. S. Wong, I. Ensminger, S. Garrity, D. Y. Hollinger, A. Noormets, and J. Peñuelas. 2016. A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers. Proceedings of the National Academy of Sciences of the United States of America 113:13087–13092.

German, L. 2004. Ethnoscientific understandings of Amazonian Dark Earths. Pages 179–201 *in* J. Lehmann, D. Kern, B. Glaser, and W. I. Wood, editors. Amazonian dark earths: origins, properties, management. Springer Science, Dordrecht, The Netherlands.

Gitelson, A. A., Y. J. Kaufman, R. Stark, and D. Rundquist. 2002. Novel algorithms for remote sensing estimation of vegetation fraction. Remote Sensing of Environment 80:76–87.

Glaser, B., and J. J. Birk. 2012. State of the scientific knowledge on properties and genesis of Anthropogenic Dark Earths in Central Amazonia (terra preta de Índio). Geochimica Et Cosmochimica Acta 82:39–51.

Glaser, B., L. Haumaier, G. Guggenberger, and W. Zech. 2001. The ‘Terra Preta’ phenomenon: a model for sustainable agriculture in the humid tropics. Naturwissenschaften 88:37–41.

Glaser, B., W. Zech, and W. I. Woods. 2004. History, current knowledge and future perspectives of geoecological research concerning the origin of Amazonian anthropogenic dark earths (Terra Preta). Pages 9–17 *in* B. Glaser and W. I. Woods, editors. Amazonian Dark Earths: explorations in space and time. Springer-Verlag, Berlin, Germany.

Goulding, M., N. J. H. Smith, and D. J. Mahar. 1996. Floods of fortune: ecology & economy along the Amazon. Columbia University Press, New York City, New York, USA.

Hagen, S. C., B. H. Braswell, S. Frolking, W. A. Salas, and X. Xiao. 2002. Determination of sub-pixel fractions of non-forested area in the Amazon using multi-resolution satellite data. Journal of Geophysical Research: Atmospheres 107:LBA16–11.

Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–853.

Heckenberger, M. J. 2004. The ecology of power; culture, place and personhood in the Southern Amazon, AD 1000–2000. Routledge, Oxon, UK.

Heckenberger, M. J., C. Fausto, and B. Franchetto. 2003*b*. Revisiting Amazonia circa 1492, Letters. Science 302:2068–2069.

Heckenberger, M. J., A. Kuikuro, U. T. Kuikuro, J. C. Russell, M. Schmidt, C. Fausto, and B. Franchetto. 2003*a*. Amazonia 1492: pristine forest or cultural parkland? Science 301:1710–1714.

Heckenberger, M. J., J. C. Russell, C. Fausto, J. R. Toney, M. J. Schmidt, E. Pereira, B. Franchetto, and A. Kuikuro. 2008. Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon. Science 321:1214–1217.

Henige, D. 1998. Numbers from nowhere: the American Indian contact population debate. University of Oklahoma Press, Norman, Oklahoma, USA.

Houghton, R. A., K. T. Lawrence, J. L. Hackler, and S. Brown. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Global Change Biology 7:731–746.

Howey, M. C. L., M. Palace, and C. M. McMichael. 2016. A geospatial modeling approach to monument construction using Michigan from AD 1000–1600 as a case study. Proceedings of the National Academy of Sciences of the United States of America 113:7443–7448.

Junqueira, A. B., G. H. Shepard, and C. R. Clement. 2011. Secondary forests on anthropogenic soils of the Middle Madeira River: valuation, local knowledge, and landscape domestication in Brazilian Amazonia. Economic Botany 65:1–15.

Justice, C. O., et al. 1998. The moderate resolution imaging spectroradiometer (MODIS): land remote sensing for global change research. IEEE Transactions on Geoscience and Remote Sensing 36:1228–1249.

Keller, M. A., et al. 2004. Ecological research in the large-scale biosphere atmosphere experiment in Amazonia (LBA): early results. Ecological Applications 14:S3–S16.

Kern, D., M. Lim da Costa, and F. J. L. Frazão. 2004. Evolution of the scientific knowledge regarding archaeological Black Earths of Amazonia. Pages 19–28 *in* B. Glaser and W. I. Woods, editors. Amazonian Dark Earths: explorations in space and time. Springer-Verlag, Berlin, Germany.

Lepine, L. C., S. V. Ollinger, A. P. Ouimette, and M. E. Martin. 2016. Examining spectral reflectance features related to foliar nitrogen in forests: implications for broad-scale nitrogen mapping. Remote Sensing of Environment 173:174–186.

Levis, C., et al. 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. Science 355:925–931.

Malhi, Y., L. E. O. C. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, and P. Meir. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences of the United States of America 106:20610–20615.

Marschner, P. 1995. Mineral nutrition of higher plants. Academic Press, New York, New York, USA.

Martin, M. E., and J. D. Aber. 1997. High spectral resolution remote sensing of forest canopy lignin, nitrogen and ecosystem processes. Ecological Applications 7:431–443.

McGovern, P. E. 1995. Science in archaeology: a review. American Journal of Archaeology 99:79–142.

McMichael, C. H., A. Correa-Metrio, and M. B. Bush. 2012*b*. Pre-Columbian fire regimes in lowland tropical rainforests of southeastern Peru. Palaeogeography, Palaeoclimatology, Palaeoecology 342–343: 73–83.

McMichael, C. M., F. Matthews-Bird, W. Farfan-Rios, and K. J. Feeley. 2017. Ancient human disturbances may be skewing our understanding of Amazonian forests. Proceedings of the National Academy of Sciences of the United States of America 114:522–527.

McMichael, C. M., M. W. Palace, M. B. Bush, B. Braswell, S. Hagen, E. G. Neves, M. R. Silman, E. K. Tamanaha, and C. Czarnecki. 2014*a*. Predicting pre-Columbian anthropogenic soils in Amazonia. Proceedings of the Royal Society B 281:1777.

McMichael, C. H., M. Palace, and M. Golightly. 2014*b*. Bamboo-dominated forests and pre-Columbian earthwork formations in southwestern Amazonia. Journal of Biogeography 41:1733–1745.

McMichael, C. H., D. R. Piperno, M. B. Bush, M. R. Silman, A. R. Zimmerman, M. F. Raczka, and L. C. Lobato. 2012*a*. Sparse pre-Columbian human habitation in western Amazonia. Science 336: 1429–1431.

McMichael, C. M., D. R. Piperno, E. G. Neves, M. B. Bush, F. O. Almeida, G. Mongeló, and M. B. Eyjolfsdottir. 2015. Phytolith assemblages along a gradient of ancient human disturbance in western Amazonia. Frontiers in Ecology and Evolution 3:141.

Medina, J. T. 1934. Carvajal's account. Pages 167–242 *in* H. C. Heaton, editor. [1542] The discovery of the Amazon according to the account of Friar Gaspar de Carvajal and other documents, compiled by J. T. Medina. Special publication no 17. American Geographical Society, New York, New York, USA.

Meggers, B. J. 1954. Environmental limitations on the development of culture. American Anthropologist 56:801–824.

Meggers, B. J. 1971. Amazonia: man and culture in a counterfeit paradise. Harlan Davidson, Wheeling, Illinois, USA.

Meggers, B. J. 2003. Revisiting Amazonia circa 1492, Letters. Science 302:2067.

Moran, E. 1974. The adaptive system of the Amazonian Caboclo. Pages 136–159 *in* A. Linton and C. Wagley, editors. Man in the Amazon. Columbia University Press, New York City, New York, USA.

Morcote-Ríos, G., and R. Bernal. 2001. Remains of palms (*Palmae*) at archaeological sites in the New World: a review. Botanical Review 67:309–350.

Morton, D. C., J. Nagol, C. C. Carabajal, J. Rosette, M. Palace, B. D. Cook, E. F. Vermote, D. J. Harding, and P. R. North. 2014. Amazon forests maintain consistent canopy structure and greenness during the dry season. Nature 506:221–224.

Neves, E. 1999. Changing perspectives in Amazonian archaeology. Pages 220–249 *in* G. G. Politis and B. Alberti, editors. Archaeology in Latin America. Routledge, New York, New York, USA.

Neves, E. G., V. L. Guapindaia, H. Lima, B. L. Costa and J. Gomes. 2014. A tradição Pocó-Açutuba e os primeiros sinais visíveis de modificações de paisagens na calha do Amazonas. Portada: Selva amazónica desde el cielo (foto S. Rostain) Contraportada: Detalle del primer mapa del Amazonas, de Quito al Océano Atlántico por el Jesuita Cristóbal de Acuña para el Rey en 1642:137.

Neves, E., and J. Petersen. 2006. Political economy and Pre-Columbian landscape transformations in Central Amazonia. Pages 279–310 *in* W. L. Balée and C. L. Erickson, editors. Time and complexity in historical ecology: studies in the neotropical lowlands. Columbia University Press, New York, New York, USA.

Neves, E. G., J. B. Petersen, R. N. Bartone, and M. J. Heckenberger. 2004. The timing of *terra preta* formation in the central Amazon: archaeological data from three sites. Pages 125–133 *in* B. Glaser and W. I. Woods, editors. Amazonian Dark Earths: explorations in space and time. Springer-Verlag, Berlin, Germany.

Nevle, R. J., D. K. Bird, W. F. Ruddiman, and R. A. Dull. 2011. Neotropical human–landscape interactions, fire, and atmospheric CO_2 during European conquest. Holocene 21:853–864.

Nicotra, A. B., M. Hofmann, K. Siebke, and M. C. Ball. 2003. Spatial patterning of pigmentation in evergreen leaves in response to freezing stress. Plant Cell and Environment 26:1893–1904.

Nobre, C., P. J. Sellers, and J. Shukla. 1991. Amazonian deforestation and regional climate change. Journal of Climate 4:957–988.

Olson, D. M., et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51:933–938.

Palace, M., M. Keller, G. P. Asner, S. Hagen, and B. Braswell. 2008. Amazon forest structure from IKONOS satellite data and the automated characterization of forest canopy properties. Biotropica 40:141–150.

Palace, M., M. Keller, G. C. Hurtt, and S. Frolking. 2012. A review of above ground necromass in tropical forests. Pages 215–252 *in* P. Sudarshana, M. Nageswara-Rao, and J. R. Soneji, editors. Tropical forests. Intech, Winchester, UK (online publication).

Pellissier, P., S. Ollinger, L. Lepine, M. Palace, and W. McDowell. 2015. Remote sensing of foliar nitrogen in cultivated grasslands of human dominated landscapes. Remote Sensing for Environment 167:88–97.

Petersen, J., E. Neves, and M. Heckenberger. 2001. Gift from the past: terra preta and prehistoric Amerindian occupation in Amazonia. Pages 86–105 *in* C. McEwen, C. Bareto, and E. Neves, editors. Unknown Amazon: culture in nature in ancient Brazil. British Museum Press, London, UK.

Petorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20:503–510.

Phillips, S. J., R. P. Anderson, and R. E. Schapired. 2006. Maximum entropy modeling of species geographic distribution. Ecological Modelling 190: 231–259.

Piperno, D. R., C. H. McMichael, and M. B. Bush. 2015. Amazonia and the Anthropocene: What was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? Holocene 25:1588–1597.

Poorter, L., et al. 2016. Biomass resilience of Neotropical secondary forests. Nature 530:211–214.

Prestes-Carneiro, G., P. Béarez, S. Bailon, A. R. Py-Daniel, and E. G. Neves. 2016. Subsistence fishery at Hatahara (750–1130 CE), a pre-Columbian central Amazonian village. Journal of Archaeological Science: Reports 8:454–462.

Quesada, C., J. Lloyd, L. O. Anderson, N. M. Fyllas, M. Schwarz, and C. I. Czimczik. 2011. Soils of Amazonia with particular reference to the RAINFOR sites. Biogeosciences 8:1415–1440.

Quintero-Vallejo, E., Y. Klomberg, F. Bongers, L. Poorter, M. Toledool, and M. Peña-Claros. 2015. Amazonian dark Earth shapes the understory plant community in a Bolivian forest. Biotropica 47:152–161.

Rice, A. H., E. H. Pyle, S. R. Saleska, L. Hutyra, M. Palace, M. Keller, P. B. de Camargo, K. Portilho, D. F. Marques, and S. C. Wofsy. 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecological Applications 14:s55–s71.

Roosevelt, A. C. 1991. Moundbuilders of the Amazon: geophysical archaeology on Marajo Island. Academic Press, San Diego, California, USA.

Saatchi, S. S., R. A. Houghton, R. C. Dos Santos Alvala, J. V. Soares, and Y. Yu. 2007. Distribution of aboveground live biomass in the Amazon basin. Global Change Biology 13:816–837.

Saatchi, S., M. Marlier, D. Clark, R. Chazdon, and A. Russell. 2011. Impact of spatial variability of forest structure on radar estimation of aboveground biomass in tropical forests. Remote Sensing of Environment 115:2836–2849.

Salati, E., and P. Vose. 1984. Amazon basin: a system in equilibrium. Science 225:129–138.

Schmidt, M. J., et al. 2014. Dark earths and the human built landscape in Amazonia: a widespread pattern of anthrosol formation. Journal of Archaeological Science 42:152–165.

Simard, M., N. Pinto, J. B. Fisher, and A. Baccini. 2011. Mapping forest canopy height globally with spaceborne lidar. Journal of Geophysical Research: Biogeosciences 116:G04021.

Smith, N. 1980. Anthrosols and human carrying capacity in Amazonia. Annals of the Association of American Geographers 70:553–566.

Söderström, M., J. Eriksson, C. Isendahl, D. P. Schaan, P. Stenborg, L. Rebellato, and K. Piikki. 2016. Sensor mapping of Amazonian Dark Earths in deforested croplands. Geoderma 281:58–68.

Sombroek, W., D. Kern, T. E. Rodrigues, M. da Silva Cravo, T. J. Cunha, W. Woods and B. Glaser. 2002. Terra preta and Terra mulata: pre-Columbian Amazon kitchen middens and agricultural fields, their sustainability and their replication. *In* 17th World Congress of Soil Science, 14–21 August 2002, Thailand.

ter Steege, H., et al. 2013. Hyperdominance in the Amazonian tree flora. Science 342:1243092.

Terborgh, J. 1992. Maintenance of diversity in tropical forests. Biotropica 24:283–292.

Tian, H., J. M. Melillo, D. W. Kicklighter, A. D. McGuire, J. Helfrich III, B. Moore III, and C. J. Vorosmarty. 2000. Climatic and biotic controls on annual carbon storage in Amazonian ecosystems. Global Ecology and Biogeography 9: 315–335.

Treuhaft, R., F. Gonçalves, J. R. dos Santos, M. Keller, M. Palace, S. N. Madsen, F. Sullivan, and P. M. L. A. Graça. 2015. Tropical-forest biomass estimation at X-Band from the Spaceborne TanDEM-X interferometer. IEEE Geoscience and Remote Sensing Letters 12:239–243.

Urrego, D. H., M. B. Bush, M. R. Silman, B. A. Niccum, P. La Rosa, C. H. McMichael, S. Hagen, and M. Palace. 2013. Holocene fires, forest stability and human occupation in south-western Amazonia. Journal of Biogeography 40:521–533.

Ustin, S., D. Roberts, J. Gamon, G. Asner, and R. Green. 2004. Using imaging spectroscopy to study ecosystem processes and properties. BioScience 54:523–534.

Werth, D., and R. Avissar. 2002. The local and global effects of Amazon deforestation. Journal of Geophysical Research: Atmospheres 107:LBA 55-1–LBA 55-8.

WinklerPrins, A. M. G. A., and S. P. Aldrich. 2010. Locating Amazon dark Earths: creating an interactive GIS of known locations. Journal of Latin American Geography 9:33–50.

Woods, W. I. 2003. Development of anthrosol research. Pages 3–14 *in* J. Lehmann, D. Kern, B. Glaser, and W. I. Wood, editors. Amazonian Dark Earths: origins, properties, management. Springer Science, Dordrecht, The Netherlands.

Woods, W. I., and J. M. McCann. 1999. The Anthropogenic origin and persistence of Amazonian dark Earths. Yearbook, Conference of Latin American Geographers 25:7–14.

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